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Maintenance of quality in fish eggs and larvae collected during plankton hauls

E. H. Ahlstrom[1]

The quality of preserved fish eggs and larvae in marine zooplankton collections is discussed in this section, as well as all the steps in the chain of events between collection, preservation and handling at sea, and sorting, identification, handling and storage ashore which could influence the quality of fish eggs and larvae, either adversely or favourably.

Careful examination has been made of fish eggs and larvae from a variety of sources, including material from all the oceans. Well-preserved collections have been in the minority. In many collections the condition of specimens ranged from fair to almost unrecognizable.

In some collections damage to specimens was due to the preservative which was either too strong (4 per cent formaldehyde or even stronger), or which had additives for buffering or colour retention which caused deterioration of quality (as for example, hexamine). In most instances, however, the poor quality of the specimens was not primarily due to the preservative but to collection techniques, delay in fixation, and incorrect handling of the material in the laboratory. There is ample evidence, however, which shows clearly that first-rate quality can be maintained in preserved fish eggs and larvae over an extended period of time.

Some stages of fish larvae are more fragile and subject to greater damage during collection and handling than other stages. As a rule, younger stages of fish larvae, i.e. yolk-sac larvae and small larvae prior to fin formation are more fragile and subject to greater damage during collection and handling than older stages of larvae. Some kinds of fish larvae are fragile at all stages. Thus, thin elongate larvae such as clupeids, engraulids, or stomiatoids are usually more easily damaged (gut torn, eyes lost, etc.) than compact stubby larvae such as carangids, scorpaenids and serranids. Early stage eggs (between fertilization and blastopore closure) are more subject to damage during collection than middle and late stage eggs.

Fish eggs and larvae in collections from tropical regions usually are in poorer condition, on the average, than fish eggs and larvae collected and handled in comparable fashion from temperate or subarctic regions.

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The poorer quality of fish larvae collected from tropical regions could be due, in part, to the temperature related phenomenon of more rapid deterioration of specimens that die during the course of a haul in tropical waters. This is at present only a supposition, but related to better substantiated observations of the adverse effects of delay, even of minutes, in preservation of plankton collections after the net has been retrieved aboard the vessel. The influence of duration of tow on quality of specimens in tropical regions should be critically evaluated. Perhaps in tropical waters, the time duration of a haul should be decreased and the number of hauls increased.

Collection at sea

Some aspects of quantitative sampling of fish eggs and larvae have little influence on quality of the specimens obtained; these would include such items as the need to cover the entire depth range of the eggs and larvae of the fishes being investigated, the need for uniformity in gear deployment and for freedom from clogging during a haul. The critical problem area in sampling as regards quality is that of net avoidance by larvae. To decrease this, there has been a trend to increase speed of hauling. However, the value of the increased catch of larger larvae has to be weighed against two adverse effects of increased speed: increased loss of small eggs and larvae through the mesh apertures of the net due to increased filtration pressure at higher speeds (the extrusion problem) and poorer condition of the specimens retained.

Detailed personal observations on the quality of fish eggs and larvae as related to vessel speed were made on collections from the standard CalCOFI net (Ahlstrom, 1952), paired Brown-McGowan BONGO nets (McGowan and Brown, 1966), Gulf III sampler (Gehringer, 1952), Gulf V sampler (Arnold, 1959), Clarke jet-net (Clarke, 1964), Bary high-speed plankton sampler (Bary *et al.*, 1958). The unencased nets (CalCOFI, BONGO, and Gulf V) were hauled at speeds between about 1.5 to 5 knots, while the encased nets (Gulf III, jet, and Bary) were hauled at speeds between about 2 to 8.5 knots. For all gears, fish eggs and larvae were in the best condition from hauls made at slow vessel speeds, and damage to specimens became increasingly greater with increase in speed of hauling. Filtration pressure on eggs and larvae resulting from increased towing speeds may be the most critical factor influencing quality of fish eggs and larvae at the time of collection. Such observations of damage resulting from increased towing speeds are not unique to fish eggs and larvae. Tranter and associates, for example, recorded progressive damage to appendicularia between hauling speeds of 1.5 and 2.4 m/sec (Tranter and Smith, 1968).

Where hauls have been made at slow vessel speeds, or taken vertically with such gear as the Hensen egg net or the standard IIOE net (Currie, 1963) it may be assumed that fish eggs and larvae would be brought aboard within the retrieved net in good condition, and the following comments are made for fish eggs and larvae in that state.

Preservation

After the net is brought aboard it is washed down to dislodge organisms clinging to the meshes of the net. Water pressure should be sufficient to wash down the net, but not so strong as to damage specimens. This is another danger point. The cod-end bucket or sac containing the plankton sample is detached and the sample is preserved at once. Delay in preservation can be a critical factor with regard to quality of the material.

The following details illustrate the adverse effects of delay in preserving plankton collections.

While checking over the fish eggs and larvae from the southern pattern of a CalCOFI cruise in the late 1950s it was noted that about half of the collections were showing serious deterioration with many larvae too disintegrated to identify or to measure. On investigation, all the poor collections were found to have been taken on one of the two scientific watches. The scientist-in-charge, when questioned, admitted that there had been a time delay of about 20 min in preserving samples. The effect of this delay on the condition of fish eggs and larvae was disastrous.

The following methods are used at the National Marine Fisheries Service, La Jolla.

Samples are preserved in quart (946 ml) jars. The plankton is emptied into the jar and the residue of plankton in the cod-end bucket is washed down into the jar. The jar should be at least three quarters full before formaldehyde is added. Then add 50 ml of concentrated commercial formaldehyde (40 per cent), followed by 20 ml of a saturated solution of borax in sea-water, and the jar is then filled to the top with sea-water before capping, after which it is gently inverted a few times to ensure thorough mixing of the fixative with the specimens. The final concentration of the formaldehyde is about 2.2 per cent. This concentration is not necessarily put forward as the optimal amount for preservation of fish eggs and larvae but it produces good quality preserved specimens, and has proved to be satisfactory for many years.

Jars containing plankton should always be completely filled (Parts I and V), otherwise the concentration of formaldehyde may be altered when using the above method of fixation. The contents will also slosh about when the ship rolls, thus damaging fragile fish larvae.

In order to preserve natural colour in biological specimens, investigators have added antioxidants such as emulsified concentrate of Butylated Hydroxytoluene (BHT) (Waller and Eschmeyer, 1965), Butylated Hydroxyanisole (BHA), (Toyama and Miyoshi, 1963) and Sodium Ascorbate (Yoshida, 1962). Red pigments have been shown to be important in identification of tuna larvae (Ueyanagi, 1966; Matsumoto *et al.*, 1972). Dr W. J. Richards (NMFS, Southeast Fisheries Center) (personal communication), reports variable success with BHT in preserving red pigments in fish larvae, particularly tunas, after extensive tests, and finds that the best procedure for studying evanescent pigment in fish larvae is to examine specimens immediately after collection and preservation.

Storage of collections aboard the research vessel

To minimize damage to delicate organisms during storage on the vessel, samples should be stored in the most stable part of the vessel. Temperature of storage may be important, particularly in tropical regions. This, again, has been one of the uncontrolled variables that might effect specimen quality. Experiments are needed to test the effect of storage temperature on the condition of plankton organisms, especially during cruises of rather long duration.

Handling the collections ashore

PLANKTON VOLUME DETERMINATIONS

Not all laboratories make a plankton volume determination as the first shore-side step in processing a plankton collection, but many do, including our laboratory. This measurement is of value as a rough measure of zooplanktonic biomass, but the determination also has a practical value in subsequent handling of the collection. Large samples may have to be aliquoted and the fraction to be sorted will often depend on sample size.

Damage to specimens during handling for volume determination should be minimal. The plankton is separated from the preserving liquid by pouring the sample through a fine-meshed draining cone. The plankton is retained in the cone until drainage of liquid from the cone diminishes to an occasional drop. The volume of drained plankton is determined by measuring the change in volume of a partly filled graduated cylinder on its addition. The sample is again filtered to concentrate it, and returned to a preserving liquid. At this time, it is advisable to place the sample in new 2 per cent formaldehyde solution rather than return the sample to its original preserving liquid (Parts I and V). The practice at La Jolla has been variable in this respect.

SORTING

At our laboratory, separation of fish eggs and larvae from the other plankton constituents has top priority, and this is done before any other organisms are removed. Usually the total sample is sorted for eggs and larvae. Because of the danger of formaldehyde poisoning, the plankton is separated from its preservative and placed in fresh water for sorting. Deterioration of quality can occur if plankton is kept too long in fresh water. Fortunately, most samples of fish eggs and larvae can be completely sorted during 1 day. The fish eggs and larvae are placed in vials, preferably 2-dram, and preservative added. We use 1.05 per cent buffered formaldehyde, prepared with tap or distilled water. The plankton is returned to its preserving liquid.

When sorting of a sample is not completed during a working day, the sorted portion is kept separate from the unsorted, but preservative is added to each. The sample should not be allowed to remain in fresh water overnight although, unfortunately, this sometimes happens. Occasionally samples require several days to sort. If allowed to remain in fresh water without preservative for this length of time, marked deterioration could result. The problem is compounded by holidays or week-ends. Unless carefully monitored, more damage to specimens can occur during sorting in fresh water than during any other shoreside operation (Parts V and VI).

IDENTIFICATION

During identification of eggs and larvae, the preservative is retained in the sample (1.05 per cent buffered formaldehyde); hence the problems outlined for sorting in fresh water do not exist. If an investigator is ultra-sensitive to formalin the larvae can be transferred to ethanol or similar preservative. Damage to specimens can result from handling with forceps or while measuring, but such damage is minimized by experienced workers. Unless damage to specimens results from the preservative itself, which can act beyond this step during subsequent storage of specimens, the quality of the preserved material will have been determined by preceding events (already discussed) by the time the collection reaches the ichthyoplanktologist for identification and study.

At this step, many kinds of fish eggs and larvae are separately bottled, and, of course, put in fresh preservative. Usually the eggs or larvae occupy only a small percentage of the container volume, hence the proportion of preserving liquid to organisms is large. Unquestionably, this is advantageous with regard to maintenance of quality during storage. While preparing this section, I have examined collections of larvae at our laboratory stored for 15 to 20 years. The larvae remain in excellent condition, with melanistic pigment still intense. There has been no observable deterioration of quality, and it follows from this that 1.05 per cent buffered formaldehyde in fresh water has proved itself to be a quality preservative for fish eggs and larvae.

STORAGE

A chief concern in curating identified collections of fish eggs and larvae is to prevent loss of specimens due to drying up. For 'dead' storage of specimens, such loss can be minimized if groups of vials containing specimens are stored in a bath of preservative within air-tight jars. Most of the Dana material at Charlottenlund (Denmark) is so curated. For collections that are consulted frequently, as in our eggs and larvae collection at La Jolla, this method of storage is impractical, due to the difficulty of retrieval. Our collection is curated for ready retrieval of any desired collection. Specimens are mostly stored in 2 dram (7.39 ml) vials sealed with a plastic cap that has an inner vinyl liner that permits firm sealing. We store the vials in cardboard boxes designed to snugly accommodate 60. Collections must be examined periodically and preservative added. Some years ago we used corks for stoppers in vials. Although corks permit a good seal, they have the disadvantage of discolouring the larvae in some collections.

We have not investigated one aspect of storage—change in concentration of the preservative due to evaporation. When the preserving liquid is reduced by half due to evaporation, has the effect been to double the strength of formalin in the vial, or is formaldehyde lost along with water vapour during evaporation? This is an important point to settle. Perhaps in curating for evaporation, the old preserving liquid should be removed and new preservative added.

Specimens should be stored away from light. They lose even melanistic pigment if allowed to remain in the light for a period of time.

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BULLETIN OF MARINE SCIENCE, 26(3): 285–402, 1976

PELAGIC STROMATEOID FISHES (PISCES, PERCIFORMES) OF THE EASTERN PACIFIC: KINDS, DISTRIBUTIONS, AND EARLY LIFE HISTORIES AND OBSERVATIONS ON FIVE OF THESE FROM THE NORTHWEST ATLANTIC

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ABSTRACT

This contribution has a dual purpose: first, to establish the kinds of pelagic stromateoid fishes present in the eastern Pacific, including their distribution and relative abundances and second, to describe their early life histories. Complete life history series are available for 11 species: *Amarsipus carlsbergi* (Amarsipidae); *Icichthys lockingtoni* (Centrolophidae); *Tetragonurus atlanticus* and *T. cuvieri* (Tetragonuridae); and *Cubiceps caeruleus, C. pauciradiatus, Psenes arafurensis, P. cyanophrys, P. maculatus, P. pellucidus*, and *P. sio* (Nomeidae). Fragmentary series, sometimes restricted to a few specimens, are available for eight species: *Schedophilus huttoni, S. labyrinthicus, S. maculatus* (Centrolophidae); *Tetragonurus pacificus* (Tetragonuridae); and *Cubiceps capensis, Cubiceps* sp. A, *Cubiceps* sp. B, and *Nomeus gronovii* (Nomeidae). Fishes in the families Amarsipidae and Nomeidae and two species of the Tetragonuridae are primarily distributed in tropical-subtropical waters; those in the family Centrolophidae and *T. cuvieri* are largely temperate water forms.

In treating life history series, the dynamic approach of tracing developmental characters is used. For each species the following items are discussed: literature, material, distribution, distinguishing characters of juveniles and of larvae, meristics, morphometrics, ossification, and pigmentation. The importance of skeletal characters such as the number of vertebrae, possession of both a haemal spine and ribs on one to several vertebrae, the number and positioning of predorsal bones in relation to neural spines and of pterygiophores in relation to neural and haemal spines is discussed for all species. The pelagically developing eggs are known for six species, *Icichthys lockingtoni*, *Tetragonurus cuvieri*, *T. atlanticus*, *Cubiceps pauciradiatus*, *C. caeruleus*, and *Psenes sio*, and are tentatively identified for two others, *Psenes pellucidus* and *P. arafurensis*. *Cubiceps carinatus* Nichols and Murphy from the eastern Pacific is considered a synonym of *C. pauciradiatus* Günther which has a worldwide tropical-subtropical distribution.

In a critical review of stromateoid fishes, Haedrich (1967) recognized five families and 14 genera. Subsequently, Haedrich (1969) added another family, Amarsipidae, and genus *Amarsipus*. Fishes in three of the six stromateoid families are exclusively oceanic as follows: Family Amarsipidae (monotypic—*Amarsipus carlsbergi*), family Tetragonuridae (one genus *Tetragonurus*, three species), and family Nomeidae (three genera—*Nomeus* [one species], *Cubiceps* [ca. seven species], *Psenes* [ca. six species]). Fishes in the family Ariommidae (one genus *Ariomma*) are oceanic and coastal. Fishes in the family Centrolophidae with six genera, have two genera (*Centrolophus* and *Icichthys*) exclusively oceanic, one genus (*Schedophilus*) a mixture of oceanic and coastal species, and three genera (*Hyperoglyphe*, *Seriolella*, and *Psenopsis*) exclusively coastal. Fishes of the family Stromateidae (three genera, *Stromateus*, *Peprilus*, and *Pampus*) are coastal. Hence, of the 15 genera of stromateoid fishes, seven are exclusively oceanic, two are mixed oceanic and coastal, and six are exclusively coastal.

Citations for previous records of occurrences of pelagic stromateoid fishes from the eastern Pacific Ocean will be given in the accounts of the families, genera, and species. The taxonomy of the nomeid fishes has been inadequately known, although recent contributions of Haedrich, particularly Haedrich (1967, 1972) have aided in clarifying the species composition. Haedrich showed that most species of nomeids are widely distributed in the three major oceans, and that the majority of nominal species described previously have to be relegated to the synonymy of about 14 species. Two species described from the eastern Pacific, *Psenes pacificus* Meek and Hildebrand and *Cubiceps carinatus* Nichols and Murphy have to be placed in the synonymy of *P. cyanophrys* Cuvier and Valenciennes and *C. pauciradiatus* Günther, respectively. Despite several eastern Pacific records for *Cubiceps gracilis* (Berry and Perkins, 1966; Fitch and Lavenberg, 1968; Lavenberg and Fitch, 1966), it is quite doubtful that this species occurs in the North Pacific, and Haedrich (1972) referred Japanese specimens reported by Abe (1955b) as *C. gracilis* to *C. caeruleus*.

The early life history stages are inadequately known for most oceanic stromateoid fishes. They have been best worked out for the three species of *Tetragonurus* (Grey, 1955), for one centrolophid, *Centrolophus niger* (Sanzo, 1932) and for two nomeids, *Cubiceps gracilis* (Sparta, 1946), and *Psenes cyanophrys* (Legaspi, 1956).

This paper has a dual purpose: (1) to establish the kinds of pelagic stromateoid fishes in the eastern Pacific together with their distribution and relative abundance, and (2) to describe the early life history stages of most of these. Observations on Atlantic material are included for larvae and early juveniles of the following species of nomeids: *Nomeus gronovii*, *Cubiceps pauciradiatus*, *Psenes maculatus*, *P. cyanophrys*, and *P. pellucidus*.

The families and species to be dealt with are as follows (see Table 1 for their meristics):

Family Amarsipidae
  Amarsipus carlsbergi Haedrich, 1969
Family Centrolophidae
  Icichthys lockingtoni Jordan and Gilbert, 1880
  Schedophilus huttoni (Waite, 1910)
  Schedophilus labyrinthicus McAllister and Randall, 1975
  Schedophilus maculatus Günther, 1860
Family Tetragonuridae
  Tetragonurus atlanticus Lowe, 1839
  Tetragonurus cuvieri Risso, 1810
  Tetragonurus pacificus Abe, 1953
Family Nomeidae
  Cubiceps caeruleus Regan, 1914
  Cubiceps capensis (Smith, A., 1849)
  Cubiceps pauciradiatus Günther, 1872
  Cubiceps sp. A (tropical)
  Cubiceps sp. B (central water mass)
  Nomeus gronovii (Gmelin, 1788)
  Psenes arafurensis Günther, 1889
  Psenes cyanophrys Cuvier and Valenciennes, 1833
  Psenes maculatus Lütken, 1880
  Psenes pellucidus Lütken, 1880
  Psenes sio Haedrich, 1970

MATERIALS AND METHODS

Our primary source of life history series has been the collections of fish eggs and larvae sorted from plankton hauls taken on cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) including extended offshore coverage on CalCOFI cruises 7205 and 7210 and cruises made into the Gulf of California; collections taken on EASTROPAC and subsequent cruises in the tropical eastern Pacific; collections made on expeditions conducted by Scripps Institution of Oceanography (SIO) including SHELLBACK (S.B.), NORPAC, CATO II, ARIES 9, STEP 1, and CLIMAX II; collections made off Hawaii on TOWNSEND CROMWELL (T.C.) cruise 32 and at the station off Hawaii sampled repeatedly by Thomas Clarke (Clarke, 1973). These have been supplemented by specimens from the western North Atlantic.

The primary sources of juveniles and adult specimens have been from midwater trawl hauls made on cruises of the National Marine Fisheries Service (NMFS) in the eastern tropical Pacific, particularly TOWNSEND CROMWELL (T.C.) cruise 51 and DAVID STARR JORDAN (JORD.) cruises 57, 60, 65, and 77, from trawl hauls made on extended CalCOFI cruises 7205 and 7210, from collections made off Hawaii as given above, and from the extensive collection at SIO obtained on their numerous expeditions.

Location and date of capture are given in the tables dealing with meristics of juveniles and adults, but not in the tables dealing with morphometrics and meristics of early life history stages. These data are omitted because their inclusion would make these tables unwieldy. However, information on locality and date of sampling for these collections has been included in the Appendix.

Complete series of life history stages were established for most of the species described in this paper by the serial method of working backwards from juveniles and adults to early stage larvae before notochord flexion (i.e., preflexion stage larvae), and in some instances, to yolk-sac larvae and eggs. The dynamic approach of tracing developmental characters sequentially was used; these characters are treated in later sections.

Three developmental series of larvae and early juveniles were selected for each species as their condition and amount of material allowed. The first series, representative of the size range of specimens available for each species, was measured with an ocular microscope for morphometrics; these measurements are presented in a separate table for each species. The specimens in the second developmental series were cleared and stained following the techniques of Hollister (1934) utilizing KOH as the clearing agent for small specimens up to approximately 15 mm SL, and the techniques of Taylor (1967) using trypsin for the clearing of larger specimens for obtaining meristic data and the sequences of ossification. Either technique can be used for small speci-

Table 1. Meristics of the stromateoid fishes in the eastern Pacific

Family/Species	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pectoral fins	Pelvic fins	Caudal fin rays d Sec. + princip. + v Sec.	Branchio-stegals
Amarsipidae								
Amarsipus carlsbergi	16-18+29-31=46-48	X-XII	23-27	29-32	17-20	I,5	11-15 + 17 + 11-14	6
Centrolophidae								
Icichthys lockingtoni	23-25+34-37=58-61	41-46		27-32	18-20	I,5	11-13 + 17 + 10-13	7
Schedophilus huttoni	12+19-20=31-32	60-63		33-38	19-20	I,5	10-12 + 17 + 9-11	7
Schedophilus labyrinthicus	10+15=25	VII-VIII	26-27	III,18-19	22	I,5	11 + 17 + 10	7
Schedophilus maculatus	11+18=29	VIII-IX	27-28	III,23	21	I,5	10-11 + 17 + 10	7
Tetragonuridae								
Tetragonurus atlanticus	23-24+20-22=44-46	XIV-XV	10-12	I,9-11	17	I,5	9-10 + 17 + 9-10	6
Tetragonurus cuvieri	26-27+25-28=51-54	XV-XVIII	11-13	I-II,10-12	14-17	I,5	9-13 + 17 + 9-12	5-6
Tetragonurus pacificus	18+21-22=39-40	XI-XII	10-11	I,10-11	18	I,5	11 + 17 + 11	6
Nomeidae								
Cubiceps caeruleus	12+19=31	X-XII	I,20-23	III,20-22	20-23	I,5	7-10 + 17 + 7-10	6
Cubiceps capensis	12+19=31	X-XI	I,25	II,22 or 23	ca.21	I,5	8-9 + 17 + 8-9	6
Cubiceps pauciradiatus	13+18=31	X-XII	I,15 to 17	II,14-16	18-19	I,5	8-10 + 17 + 8-10	6
Cubiceps sp.A (tropical)	12+19=31	XI	I,22 or 23	III,21 or 22	20 or 21	I,5	12 + 17 + 12	6
Cubiceps sp.B (central water mass)	12+19=31	XI	I,19 or 20	III,20	ca.22	I,5	11-12 + 17 + 12	6
Nomeus gronovii	14+27=41	XI-XII	25-27	II,24-26	19-20	I,5	8-9 + 17 + 8-9	6
Psenes arafurensis	12+19=31	X-XI	I,20-23	III,21-23	20-21	I,5	7-10 + 17 + 7-10	6
Psenes cyanophrys	12+19=31	IX-X	I,23-26	III,23-27	19-20	I,5	7-9 + 17 + 7-9	6
Psenes maculatus	12+23=35	X-XI	I,22-23	III,21-22	19-22	I,5	8 + 17 + 8-9	6
Psenes pellucidus	13-14+27-29=40-42	XI-XII	I,26-30	III,27-30	18-20	I,5	8-10 + 17 + 8-10	6
Psenes sio	12-13+24-26=36-38	XI-XII	I,22-26	II,23-26	16-18	I,5	7-10 + 17 + 8-10	6

mens, but the KOH method has the advantage of being more rapid. This second series was less extensive inasmuch as fewer specimens could be spared for clearing and staining; the data obtained are shown in separate tables. In some cases, counts made from untreated specimens and from radiographs were included with data from cleared and stained material or used exclusively; these are noted on the pertinent tables. The third series of larvae was composed of a few select specimens to illustrate the early developmental stages of each species. The number of illustrations were limited to show the major developmental and pigmentation changes that occurred. Wherever possible, at least one specimen was illustrated of each of the three larval stages—preflexion, flexion, and postflexion, and usually several specimens of the latter stage. Also, one or more illustrations were included of early juveniles.

We separate the larval period into three stages which are associated with the development of the caudal fin and its supporting elements, and which are related directly to the morphometrics for each specimen. The three stages are termed preflexion-, flexion-, and postflexion-stage larvae, which are stages before, during, and after the upward flexing of the tip of the notochord. Before the initial development of the caudal fin in preflexion-stage larvae, and the formation of the fin in flexion-stage larvae, body length is measured as the distance from the tip of the snout to the tip of the notochord, designated as NL = notochord length. In postflexion larvae, when the caudal fin is fully formed and the notochord is completely flexed, the standard length (SL) measurement is used, i.e., the length from the tip of the snout to the posterior margin of the hypural bones. The tables of morphometrics and meristics are divided by dashed lines into three sections corresponding to each stage discussed above. We strongly support the standard use of preflexion, flexion, and postflexion stages in the measurement and description of larvae to allow for the meaningful comparisons of data.

Other measurements are defined as follows: snout to anus length is the distance from the tip of the snout along the midline to a vertical line through the posterior edge of the anus; head length (HL) is the horizontal distance from the tip of the snout to the posterior margin of the cleithrum; eye diameter is the distance across the midline of the pigmented area of the eye; snout length is the horizontal distance from the tip of the snout to the anterior margin of the pigmented region of the eye; body depth at the pectoral base is the vertical distance through the anterior margin of the pectoral base; the snout to origins of dorsal (Sn-D), anal (Sn-A), and pelvic or ventral (Sn-V) fins are distances from the tip of the snout along the midline to the vertical line through the origin of the respective fins. The body parts included in the snout to anus distance are the head and trunk. The post-anal portion of the body is simply referred to as the "tail." We try to be consistent in the use of these terms throughout the paper.

The separation of the larval period from that of juveniles and adults is not a sharp one in the stromateoid fishes as no abrupt metamorphic changes occur. However, we have used two criteria in distinguishing a larva at a transition size from a juvenile. These are: (1) the complete formation of rays in all fins, and (2) the initial development of scales. The occurrence of one or both of the above conditions was used to justify denoting a specimen as an early juvenile. Typically, the secondary caudal rays are the last fin rays to complete formation; also scale formation is seldom encountered on specimens that lack the complete complement of fin rays.

It should be mentioned that some latitude was allowed in distinguishing among larval stages. For example, we placed those specimens forming ossified caudal rays in the flexion stage, irrespective of whether the notochord had yet begun to flex or not. The size range over which transition from the postflexion larval stage to the juvenile stage occurred could seldom be precisely determined. Sometimes we lacked the critical specimens to determine the exact size at which this transition occurred; also the initiation of scale formation did not occur precisely at the same length at which fin formation was completed. Because of these uncertainties, we sometimes use postflexion in a broad sense to include early juveniles as well as postflexion-stage larvae.

Until now, the kinds of pelagic stromateoid fishes occurring in the eastern Pacific and particularly, their distribution and relative abundances, were inadequately known. To remedy this, we are including a series of tables giving information on meristics and localities of capture of juveniles and adults, and a series of distribution charts which incorporate occurrences for larvae, juveniles, and adults. In the tables mentioned above, information is included for 25 specimens of the more common species and for all available material of less common species. For the more common species, specimens included were selected to both bracket their distributions and to present a representative sampling within these ranges. Meristics were taken from X-ray radiographs, supplemented by fin counts made on the specimens. Counts included are those readily read from X-ray radiographs, i.e., vertebral counts and median fin counts. For vertebrae, the division into abdominal (precaudal) and caudal vertebrae is given as well as total counts. The last or ural centrum is included in the vertebral count. Our counts for precaudal vertebrae will not agree with many of the counts given in the literature. The difficulties resolved in discriminating between precaudal and caudal vertebrae are discussed later. Hence, we consider our information on precaudal and caudal counts of vertebrae as a significant contribution. As will become evident in our treatment of *Cubiceps*, so also is the information on the number of secondary caudal rays.

Distribution charts are presented for all species except *Cubiceps capensis*, *Schedophilus maculatus*, *S. labyrinthicus*, and *S.*

huttoni, the four species taken to the south of 20°S. The majority of our occurrence records are from the area covered on EASTROPAC cruises, i.e., between 20°N to 20°S and offshore to 126°W. Consequently, 8 of our 13 distribution charts are based on collections from this area. Of the remaining charts, two summarize occurrences of stromateoid larvae on NORPAC and extended CalCOFI cruises; one is a cumulative record of occurrences of larvae of *Icichthys lockingtoni* in the regularly occupied CalCOFI grid; and two charts show records of the nomeids that occur in the Gulf of California.

CHARACTERS OF STROMATEOID FISHES

Stromateoid fishes have a characteristic appearance. According to Haedrich (1967, p. 44) "there is no mistaking the 'stromateoid look' . . . it is a fat-nosed, wide-eyed, stuffed-up look, smug and at the same time apprehensive." Even larvae of stromateoid fishes, and especially those of nomeids, have the unmistakable stromateoid look; however, the "look" is best developed in early juveniles.

Another character common to all stromateoid fishes, except *Amarsipus*, is the presence of toothed saccular outgrowths in the pharynx immediately behind the inner gill arches. The pharyngeal sac can be seen developing on late postflexion larvae and is well formed on early juveniles of nomeids between 15 to 20 mm SL. These observations were made on cleared and stained specimens.

A third character, observed by Horn (1975) in 14 of the 15 genera of stromateoid fishes is the possession of a relatively small, euphysoclistous swim bladder which forms in preflexion larvae (3 to 5 mm) and regresses in all genera except possibly *Nomeus* before maturity. The organ is characteristic of the larval and juvenile stages which occupy surface layers in coastal and oceanic waters; according to Horn (1975), its loss accompanies changes in behavior and mode of life and is part of the transition from the juvenile to the adult stage.

In tracing early life history series it is essential to utilize characters that give an unquestionable tie between the juvenile and adult stages of a species and its postflexion larval stage. Among pelagic stromateoid fishes a number of characters can be used including meristics, sequence of fin formation, morphometrics, pigmentation, and skeletal characters. In this section we will deal primarily with meristic and skeletal characters that are of importance in distinguishing among stromateoid fishes at both the larval level and the juvenile-adult levels.

Fin Meristics

Two fins of perciform fishes tend to have stabilized counts: that for the pelvic fins is I, 5 and that for the principal caudal rays is 17 (15 branched). These counts are applicable to all the species dealt with in this paper. The number of secondary caudal rays is variable even within a species, but more so between species. The range in number of dorsal secondary caudal rays is from 7 to 15 among the species we are dealing with, and the range in number of ventral secondary caudal rays is 7 to 14. For any given species, the range in secondary caudal ray counts is 2 to 4 rays per side. The count of secondary caudal rays can be an important taxonomic character among species within a genus, e.g., *Cubiceps*.

The dorsal fin in stromateoid fishes may be divided into two fins, or it may be continuous. If divided, the first dorsal fin has 9 to 18 spines and the second dorsal fin has 0, 1, or 2 spines and 10 to 30 rays, e.g., nomeids, tetragonurids, and *Amarsipus*. In *Amarsipus* and *Tetragonurus* the spines in the first dorsal fin are much shorter than the rays in the second dorsal fin. In nomeids, the longest spines in the first dorsal fin usually are in the middle of the fin, with the spines progressively shorter both anteriad and posteriad, the posterior-most spine usually being the shortest. The spine associated with the second dorsal fin usually is longer than the terminal spine in the first dorsal fin. The continuous dorsal fin is found in the centrolophids included in this study. No attempt was made to distinguish between spines and rays in the dorsal fin in *Icichthys*. In *Schedophilus* it is sometimes difficult to distinguish between spines and rays in the continuous dorsal fin. The highest dorsal fin count among stromateoids is found in *Schedophilus huttoni* (56 to 63), a species that has been taken in the eastern South Pacific.

In stromateoid fishes the anal fin usually has about the same number of rays as the second dorsal fin, although there are some exceptions of which the most striking are found in the centrolophids. *Schedophilus labyrinthicus* has 7 or 8 more soft rays in the dorsal than in the anal fin and *S. maculatus* has 4 or 5 more rays. In *Icichthys*, where no distinction is made between spines and rays in the dorsal and anal fins, the dorsal averages 13 more elements than the anal fin. In *Amarsipus* the anal fin averages 5.5 more rays than the second dorsal. In *Tetragonurus*, the rays in the second dorsal fin average less than one more than in the anal fin. Among the 11 nomeids, the differences between dorsal and anal fin ray counts are slight, and can be higher in either fin as is shown in the following summary:

Cubiceps caeruleus	Second dorsal averages 0.5 ray more than anal fin
C. capensis	Second dorsal averages 2.5 ray more than anal fin
C. pauciradiatus	Second dorsal averages 1.25 ray more than anal fin
C. sp. A	Second dorsal averages 0.7 ray more than anal fin
C. sp. B	Second dorsal averages 0.3 ray less than anal fin
Nomeus gronovii	Second dorsal averages 0.5 ray more than anal ray
Psenes arafurensis	Second dorsal averages 1.2 ray less than anal fin
P. cyanophrys	Second dorsal and anal about equal
P. maculatus	Second dorsal averages 0.8 ray more than anal fin
P. pellucidus	Second dorsal averages 0.2 ray less than anal fin
P. sio	Second dorsal averages 0.5 ray more than anal fin

The complement of anal fin rays is preceded by 0, 1, 2, or 3 anal spines: 0 in *Amarsipus* and *Icichthys*, 1 in *Tetragonurus*, 2 in *Cubiceps pauciradiatus*, *C. capensis*, *Psenes sio*, and *Nomeus gronovii*, and 3 in the remaining species under consideration.

The pectoral fins in the species studied have ray counts of 14 to 23. Pectoral ray counts usually have a range of 2 to 4 rays between the highest and lowest counts for a species. The pectoral counts are too similar for most species to be used to distinguish among them.

There are two different sequences in which fins form in oceanic stromateoid fishes, depending primarily on whether the pelvic fins form early before the other fins, or whether they form late.

The pelvic fins are the first to form in *Psenes*, *Amarsipus*, and probably also in *Nomeus*. Among *Psenes* larvae, pelvics are present on specimens as small as 2.8 mm. When pelvics are precocious in formation in stromateoid fishes, they soon obtain their complete complement of one spine and five rays and become fairly large. In most fishes other than stromateoids that have early development of pelvic fins, there is a corresponding early development of the spines (or rays) in the anterior part of the dorsal fin. The early forming dorsal elements can become quite large and even elaborate, as for example in epinepheline serranids, gempylids, trachipterids, many bothid flatfishes and some carangids. In the stromateoids with pelvics developing first, the first dorsal is the next fin to develop, but the early forming spines are only of moderate size, never enlarged or elaborated. The other fins then form in about their regular sequence. Among stromateoids, the initiation of ray development in the caudal and pectoral fins usually slightly precedes the development of the second dorsal and anal fins. The last rays to form are usually the anterior procurrent rays of the caudal fin.

In at least three genera of stromateoid fishes from as many families, *Cubiceps*, *Tetragonurus*, and *Icichthys*, the pelvic fins are the last to initiate development. In *Cubiceps* and *Tetragonurus* the caudal fin is the first to initiate ray formation, followed by the almost simultaneous development of pectorals, second dorsal and anal fins, and somewhat later by the first dorsal and finally the pelvics. In *Icichthys* the initiation of ray formation in the pectorals precedes that of the caudal, followed by the dorsal and anal fins simultaneously, and soon thereafter, the pelvics.

Morphometrics and Pigmentation

Two of the primary characters for distinguishing among genera and species of stromateoid fishes are morphometrics and pigmentation. Morphometric tables covering the larval and early juvenile stages have been prepared for all species dealt with in this manuscript, and are treated in detail in later sections. Pigmentation patterns are best shown in illustrations, of which we include 80 of larvae and early juveniles. In addition, pigment patterns are discussed for the several species of each genus, and trenchant differences are emphasized.

Skeletal Characters

Among skeletal characters of particular relevance are (1) total number of vertebrae, (2) co-occurrence of a pair of pleural ribs and a haemal spine on each of one or more caudal vertebrae, (3) separation of vertebrae into precaudal and caudal groups, (4) position of anal fin pterygiophores in relation to haemal spines, (5) position of dorsal fin pterygiophores and predorsal bones in relation to neural spines, and (6) the supporting bones of the caudal fin.

The Vertebral Column

Number of Vertebrae.—Many centrolophids have a total count of 25 vertebrae including *Schelophilus labyrinthicus*. However, *S. maculatus* has 29 vertebrae and *S. huttoni*, 31 or 32. *Icichthys lockingtoni* has the highest vertebral count among stromateoid fishes, 58 to 61. *Amarsipus carlsbergi* has a relatively high vertebral count, 45 to 48.

The three species of *Tetragonurus* can be separated on the basis of vertebral counts alone. Our specimens of *T. pacificus* have 39 or 40 vertebrae, *T. atlanticus*, 44 to 46 and *T. cuvieri*, 51 to 54.

The most frequent, regular vertebral count among nomeids is 31; 7 of the 11 species of nomeids have this count, including all 5 species of *Cubiceps* and *Psenes arafurensis* and *P. cyanophrys*. Other total vertebral counts obtained for nomeids include 35 for *Psenes maculatus*, 36 to 38 for *P. sio*, and 40 to 42 for *P. pellucidus* and *Nomeus gronovii*.

Vertebrae usually begin to ossify during the late preflexion stage or during early flexion and all vertebrae are ossifying by early postflexion. Ossification begins at the anterior end of the axial skeleton, with neural spines ossifying before their centra—and with ossification proceeding progressively posteriad.

Ribs on Caudal Vertebrae.—In most fishes it is not difficult to separate the precaudal group of vertebrae from the caudal group, in that ribs are found only on precaudal vertebrae and haemal spines only on caudal vertebrae. This is not the case for nomeids, inasmuch as one to five caudal vertebrae (depending upon the species) bear both a haemal spine and a pair of pleural ribs.

In Table 2 the arrangement on vertebrae 12 to 19 of pairs of ribs alone, pairs of ribs and haemal spines together, and haemal spines alone is given for eight species. For *Cubiceps caeruleus*, only one vertebra, the 13th, usually bears both ribs and a haemal spine. On *Cubiceps pauciradiatus*, two vertebrae usually have both ribs and haemal spines, the 14th and 15th, although occasionally the 14th has only ribs and occasion-

Table 2. Arrangement of pairs of ribs and/or haemal spine on vertebrae 12 to 19 in nomeids (R = Ribs, H = Haemal spine)

Species	Vertebra number							
	12	13	14	15	16	17	18	19
Cubiceps caeruleus	R	R+H	H±R	H	H	H	H	H
Cubiceps pauciradiatus	R	R	R±H	R+H	H±R	H	H	H
Nomeus gronovii	R	R	R	R±H	R+H	R+H	H	H
Psenes arafurensis	R	R+H	R+H	H	H	H	H	H
Psenes cyanophrys	R	R±H	R+H	H	H	H	H	H
Psenes pellucidus	R	R	R±H	R+H	R+H	R+H	R+H	H
Psenes sio	R	R±H	R+H	R+H	R+H	H±R	H	H
Psenes maculatus	R	R+H	H	H	H	H	H	H

ally the 16th carries small ribs as well as a haemal spine. Pleural ribs are only gradually developed in a posterior direction on juveniles, as is shown for *Cubiceps pauciradiatus* (Fig. 1). The first pair of ribs associated with a haemal spine on vertebra 14 forms relatively early, but the second pair, on vertebra 15, was only beginning to form on a 55-mm specimen, but was fully developed on a 108-mm specimen. For *Nomeus gronovii*, the 16th and 17th vertebrae carry ribs and haemal spines, and occasionally the 15th also.

The problem is somewhat more complicated in *Psenes*. Both *P. arafurensis* and *P. cyanophrys* have pairs of ribs and haemal spines on the 13th and 14th vertebrae, but *P. sio* usually has four or five vertebrae bearing ribs and haemal spines (13th to 16th or 17th) and *P. pellucidus* has five (14th to 18th).

Separation of Vertebrae into Precaudal and Caudal Groups.—If the presence of both ribs and haemal spines on one to five vertebrae were the only complicating feature, it should not be too difficult to separate the precaudal from the caudal group of vertebrae. However, there is a second complicating and obfuscating factor. This results from the backward protrusion of the organs of the abdominal cavity into the space ordinarily occupied by the first several haemal spines. The resultant backward bending and crowding together of the haemal spines and ribs on these vertebrae make them difficult to interpret on radiographs. The anterior pterygiophores supporting the anal fin are also bent posteriad. The anterior-most pterygiophore is usually a large fused bone, which may bend backwards over a half dozen adjacent pterygiophores.

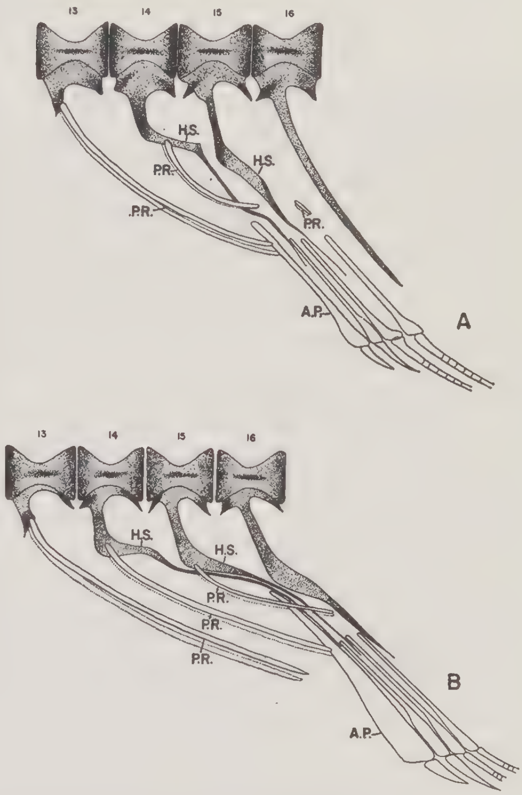

Figure 1. Lateral view of haemal spines and ribs of vertebrae 13 to 16 and interdigitation of haemal spines with the first four anal pterygiophores in *Cubiceps pauciradiatus*. A—55 mm SL; B—108 mm SL. H.S., haemal spine. P.R., pleural rib. A.P., anal pterygiophore.

We have found that the haemal spines never precede the anal fin pterygiophores, rather they interdigitate between the pterygiophores until the fin terminates. Most commonly the anterior-most haemal spine interdigitates between the first and second or second and third anal fin pterygiophores, although in *P. cyanophrys* the anterior-most haemal spine interdigitates between the fourth and fifth or fifth and sixth pterygiophores.

In specimens in which the abdominal cavity intrudes into the anal fin area, bending haemal spines, ribs and pterygiophores posteriad, and particularly in those in which the heavy anterior pterygiophore bends back over five or six adjacent pterygiophores, the interdigitation of haemal spines between anal fin pterygiophores is obviously interfered with. As a result, we find it difficult to interpret radiographs of larger specimens of nomeids, particularly specimens over 100 mm SL.

For any given species the problem of precaudal vs. caudal vertebrae can be solved if early life history stages are available. When following the sequence of ossification in a nomeid, it can be seen that the haemal spines ossify earlier than either the ribs or the pterygiophores. Because of this, separation of caudal and precaudal vertebrae can be precisely determined on cleared and stained specimens or good radiographs of postflexion larvae or early juveniles. For example, our early juveniles of *Cubiceps capensis* have the unquestioned presence of the first haemal spine on vertebra 13, hence have 12 + 19 = 31 vertebrae; however, in trying to decipher radiographs of larger juveniles, it is very difficult to tell whether the separation between precaudal vs. caudal vertebrae comes at the 13th, 14th, or 15th vertebra.

Pterygiophores

In discussing the association of fin elements, spines or rays, with their supporting pterygiophores, the element, whether a spine or ray, is, for convenience, termed a ray. Our terminology has been adopted from Eaton (1945) and Potthoff (1975). Except as noted for the anterior-most one or two rays in the dorsal and anal fins, each ray of these fins is in a serial arrangement with a pterygiophore. In addition, each fin ray secondarily articulates in a non-serial arrangement with the pterygiophore immediately posterior to it. In the majority of stromateoid fishes, the anterior-most pterygiophore of both the dorsal and anal fins supports two rays in a non-serial secondary association and is serially associated with the third ray. All succeeding rays have the dual association with pterygiophores as noted above, except that the terminal ray which serially articulates with the terminal pterygiophore, has no secondary association with a "following" pterygiophore. In larger specimens of *Cubiceps caeruleus* and *C. pauciradiatus*, a bony "stay" is associated with the last ray in a secondary association.

When the anterior-most pterygiophore of the dorsal or anal fin carries only one ray in secondary association, this pterygiophore is serially associated with the second ray of the fin, which in turn has a non-serial articulation with the second pterygiophore. All nomeids with two anal spines have only a single spinous ray in a secondary non-serial association with the first pterygiophore, which is a relatively narrow bone without evidence of fusion. In contrast, all nomeids with three anal spines carry two spinous rays in secondary association on the first broad-based pterygiophore which apparently results from the fusion of two pterygiophores during early development. The total number of pterygiophores is identical to the number of pterygiophores in serial association with rays. Thus when the anterior-most pterygiophore carries two rays in secondary association and is serially associated with the third, the number of pterygiophores is two less than the total number of rays. If the anterior-most pterygiophore carries only one ray in secondary association and is serially associated with the second ray, the number of pterygiophores is one less than the total number of rays.

Arrangement of Anal Fin Pterygiophores

Family Nomeidae (Table 3).—The sequential arrangement of anal fin pterygiophores in relation to haemal spines in nomeids is given for 13 species in Table 3. We are

Table 3. Sequential arrangement of anal fin pterygiophores in relation to haemal spines in nomeids (the pterygiophore listed immediately precedes the relevant haemal spine)

Species	Ocean	Size SL (mm)	Number of vertebrae	Anal fin	No. spines on 1st pteryg.[*]	Haemal spine on vertebra number																							Method of counts
						13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
Cubiceps pauciradiatus	P	52.0	13+18=31	II,15	1	-	1	3	4	6	7	9	10	12	14	16	frag.	-											C+S[†]
	P	78.0	13+18=31	II,15	1	-	1	3	4	6	7	9	10	12	14	16	frag.	-											C+S
	P	85.0	13+18=31	II,15	1	-	1	2	4	6	7	8	10	11	13	15	16	stay											C+S
(Type *C. carinatus*)	P	103.0	13+18=31	II,15	1	-	1	2	4	5	7	8	10	12	14	16	frag	-											X-ray[†]
Cubiceps squamiceps	I	136.0	13+18=31	III,19	2	-	?	5	6	8	9	11	12	14	15	17	18	20	-										X-ray
	I	115.0	13+18=31	III,19	2	-	?	?	7	8	9	10	12	13	15	16	18	20	-										X-ray
	I	135.0	13+18=31	III,19	2	-	?	?	7	8	9	11	13	14	16	17	19	20	-										X-ray
Cubiceps sp. B	P	17.9	12+19=31	III,20	2	1	3	5	7	9	10	12	14	15	17	19	21	1											X-ray
	P	18.7	12+19=31	III,20	2	1	3	5	7	9	10	12	14	?	?	?	?												X-ray
Cubiceps caeruleus	P	133.0	12+19=31	III,20	2	1	3	5	7	8	10	11	13	14	16	18	19	21	stay										X-ray
	P	46.0	12+19=31	III,20	2	1	3	5	7	8	10	11	13	14	16	18	19	21	stay										C+S
	P	46.0	12+19=31	III,21	2	1	3	5	7	8	10	11	13	15	16	18	20	22	stay										C+S
Cubiceps sp. A	P	14.0	12+19=31	III,22	2	2	4	6	8	10	11	13	14	16	18	20	?	?	-										X-ray
	P	19.5	12+19=31	III,22	2	2	4	6	8	10	12	13	15	17	18	20	22	23	-										X-ray
	I	43.0	12+19=31	III,21	2	2	4	6	8	10	12	13	15	17	18	20	22	-	-										X-ray
Cubiceps capensis	I	210.0	31	II,22	1	?	?	3	5	7	9	11	13	15	17	19	21	23	-										X-ray
	I	141.0	31	II,22	1	?	?	3	5	7	9	10	12	14	16	19	21	23	-										X-ray
	P	15.7	12+19=31	II,23	1	1	2	3	5	7	8	10	12	?	?	?	?	?											X-ray
Psenes arafurensis	P	28.0	12+19=31	III,22	2	1	4	6	8	9	11	12	14	16	17	19	20	23	-										X-ray
	P	117.0	12+19=31	III,23	2	2	4	6	7	9	11	13	14	16	18	19	21	23	24	-									X-ray
	P	23.2	12+19=31	III,24	2	2	4	6	8	10	12	13	15	17	19	20	22	24	25	-									C+S
Psenes cyanophrys	P	48.0	12+19=31	III,25	2	4	6	8	10	12	14	15	17	19	20	22	24	25	26	-									C+S
	P	54.0	12+19=31	III,26	2	5	6	8	10	12	13	15	17	19	20	22	24	26	27	-									C+S
	P	53.0	13+18=31	III,26	2	-	6	8	10	12	14	15	17	18	20	22	24	25	27	-									C+S
Cubiceps gracilis	A	163.0	34	III,20	2	-	?	?	5	6	8	9	11	12	14	15	17	19	20	21	-								X-ray
	A	144.0	33	III,21	2	-	?	?	5	6	8	9	11	12	14	16	17	19	21	22	-								X-ray
	A	131.0	33	III,22	2	-	?	?	5	7	8	10	11	13	15	17	18	20	22	23	-								X-ray
Psenes maculatus	A	20.4	12+23=35	III,21	2	1	3	5	6	8	9	10	12	13	14	15	17	18	19	21	22	-							X-ray
	A	22.8	12+23=35	III,22	2	1	2	5	6	8	9	10	12	13	14	15	17	18	19	21	23	-							C+S
	A	31.2	13+22=35	III,22	2	-	2	4	6	7	9	10	11	13	14	15	17	18	19	21	22	23	-						X-ray
Psenes sio	P	48.0	12+25=37	II,23	1	1	3	4	6	7	9	10	12	13	14	16	17	18	20	21	22	24	-						C+S
	P	22.5	13+25=38	II,23	1	-	1	3	5	6	8	9	10	12	13	14	16	17	19	20	21	23	24	-					C+S
	P	54.5	12+26=38	II,26	2	1	2	3	5	6	8	9	11	12	14	15	16	18	19	20	21	23	25	26	-				X-ray
Nomeus gronovii	A	45.0	15+26=41	II,26	1	-	-	-	3	5	6	8	9	11	12	13	15	16	17	19	21	22	24	26	27	-			C+S
	P	73.0	14+27=41	II,26	1	-	-	2	3	5	6	8	9	10	12	13	15	16	18	19	21	23	24	26	27	-			X-ray
	P	117.0	14+27=41	II,27	1	-	-	2	3	4	6	8	9	10	12	13	14	15	17	18	20	21	23	25	27	28	-		X-ray
Psenes pellucidus	P	35.0	13+28=41	III,29	2	-	1	3	5	7	8	10	11	13	14	15	17	18	20	21	22	23	25	26	28	30	-		X-ray
	P	35.0	13+29=42	III,30	2	-	1	3	5	7	8	10	12	13	14	15	17	18	19	21	22	23	25	26	27	29	31	-	X-ray
	P	40.0	13+29=42	III,30	2	-	1	3	5	6	8	10	11	13	14	15	17	18	19	21	22	24	25	26	28	29	31	-	C+S

[*] Anal fin spines on 1st pterygiophore are in a secondary association

[†] C+S, cleared and stained specimen; X-ray, radiograph of specimen

including information on two species that have not been taken in the eastern Pacific: *Cubiceps squamiceps* and *C. gracilis* and include Atlantic material for several of the other species. Inasmuch as species of nomeids with higher vertebral counts usually have "longer" anal fins, the species are listed in the table from low to high with regard to counts of vertebrae and for those with equal numbers of vertebrae from low to high with regard to anal fin counts.

No two species have exactly the same arrangement of anal fin pterygiophores in relation to haemal spines, although admittedly some are rather similar, particularly among *Cubiceps*. *Psenes cyanophrys* has

Table 4. Sequential arrangement of anal fin pterygiophores in relation to haemal spines in species of the Centrolophid genus *Schedophilus* (the pterygiophore listed immediately precedes the relevant haemal spine)

	Ocean	Size-SL (mm)	Number of vertebrae	Anal fin	No. spines on 1st pteryg.*	Haemal spine on vertebra number														
						11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
S. haedrichi	P	186.0	10+15=25	III,15	2	1	4	6	3	10	12	15	16	stav	-	-				
S. pemarco	A	185.0	10+15=25	III,17	2	1	4	6	9	11	13	15	18	-	-	-				
	A	188.0	10+15=25	II,17	1	1	4	6	9	11	13	15	17	18	-	-				
	A	225.0	10+15=25	III,17	2	1	4	6	9	11	13	16	18	-	-	-				
S. labyrinthicus	P	34.1	10+15=25	III,18	2	1	5	7	9	11	13	15	18	19	-					
	P	75.0	10+15=25	III,18	2	1	4	7	9	11	13	15	17	19	-					
	P	560.0	10+15=25	III,19	2	2	4	7	9	11	13	16	18	20	-					
S. ovalis	A	175.0	10+15=25	III,21	2	1	6	8	11	13	16	18	21	22	-					
	A	191.0	10+15=25	III,22	2	1	5	8	10	12	15	17	20	23	-					
S. medusophagus	A	74.0	10+15=25	II,26	2	1	4	6	9	12	15	18	20	23	26	-				
S. griseolineatus	A	195.0	10+16=26	III,22	2	1	4	6	8	10	12	14	17	19	22	23	-			
	A	200.0	10+16=26	III,21	2	1	3	6	8	10	12	14	17	19	22	-	-			
S. maculatus	P	23.0	11+18=29	III,23	2		1	4	6	8	10	12	13	15	18	20	22	24	-	-
	P	28.0	11+18=29	III,23	2		1	3	6	8	10	12	14	15	17	19	21	23	24	-
	Aust.	85.0	11+18=29	III,23	2		?	4	6	8	10	12	14	16	18	20	21	24	-	-
S. huttoni	P	24.8	12+19=31	II,31	2	-	-	1	3	6	9	11	14	16	18	21	23	26	28	31

* Anal fin spines on 1st pterygiophore are in a secondary association

the most distinctively different pattern; but all species of *Psenes* can be positively identified simply by combining axial skeletal characters with pterygiophore patterns and anal fin counts.

For most species included in this table, the precise positioning of pterygiophores and haemal spines anteriorly was determined by following the ossification of these structures in cleared and stained series of late larvae and early juveniles. For the two species for which only radiographs of larger specimens were available, *C. gracilis* and *C. squamiceps*, it was impossible to determine the precise arrangement of pterygiophores and haemal spines anterior to vertebra 16.

The anal fin pterygiophores begin to ossify on late postflexion larvae. The anterior pterygiophores ossify first, and then ossification proceeds progressively posteriad. In Table 3 a specimen is included for each of three species, *C. capensis*, *C.* sp. A, and *C.* sp. B, on which the posterior pterygiophores were not yet ossified, but the anterior pterygiophores were well formed. The *C. capensis* specimen in particular is an important one inasmuch as it shows the precise arrangement of haemal spines and pterygiophores anteriorly, an arrangement that is obscured in radiographs of the older specimens.

Genus Schedophilus (Family Centrolophidae) (Table 4).—Using the same characters for species of *Schedophilus*, equally interesting results are obtained (Table 4). We have been fortunate in seeing specimens or radiographs of eight species of *Schedophilus*, that currently are recognized as distinct species. This has made it possible for us to identify our several specimens of this genus to species. It also has convinced us of the importance of the vertebral column and associated bones (pterygiophores and predorsal bones) in the taxonomy of this group. As pointed out in the following section, the number and arrangement of predorsal bones is an important taxonomic character in the centrolophid genus *Schedophilus*.

It should be pointed out that there are two pairs of closely related species of *Schedophilus*: *S. haedrichi* (Chirichigno, 1973) recently described from the Pacific off Chile, is closely related to *S. pemarco*; similarly, *S. labyrinthicus* (McAllister and Randall, 1975), described from the central South Pacific, is closely related to *S. ovalis*. *S. haedrichi* has a lower anal count than *S. pemarco*, but a similar basic arrangement of anal fin pterygiophores in relation to haemal spines. *S. labyrinthicus* also has a lower anal count than *S. ovalis*, but a similar basic arrangement of anal fin pterygiophores vs. haemal spines. The arrangements for *S. maculatus*, *S. huttoni*, *S. medusophagus*, and *S. griseolineatus* are quite different from each other and from the above four species.

Predorsal Bones

The predorsal bones are elongate splinter bones that precede the pterygiophores that support the spines and rays of the dorsal fin: they are assumed to have originated from pterygiophores (Smith and Bailey, 1961). The usual number is three in stromateoid fishes, but some species have only two, and *Icicthys lockingtoni* may have as many as 11 or 12. The arrangement of predorsal bones is fairly stabilized among nomeids, but is quite variable among centrolophids. In point of fact, the number and arrangement of predorsal bones is an important taxonomic character in the centrolophid genus, *Schedophilus*.

The pattern encountered in most nomeids is as follows: the first of the three predorsals precedes the first neural spine, the second predorsal lies between the first and second neural spines, and the third lies between the second and third neural spines, usually accompanied by the first dorsal pterygiophore. In *Cubiceps gracilis* and *C. capensis* the first dorsal pterygiophore interdigitates between the third and fourth neural spines. The first dorsal pterygiophore is a wide (probably fused) bone that carries the anterior two spines of the first dorsal fin in a secondary association in *Cubiceps* and *Psenes*, but is slender and carries only one spine in a secondary association in *Nomeus*. Hence, the three patterns encountered in nomeids are as follows:

Usual pattern:
0/0/0 + 2/[1] found in all five species of *Psenes* and in *Cubiceps caeruleus*, *C. pauciradiatus*, *C. squamiceps*, *C.* sp. A and *C.* sp. B.
Variant:
0/0/0/2/ found in *Cubiceps gracilis* and *C. capensis.*
Variant:
0/0/0 + 1/ found in *Nomeus gronovii.*

The arrangement of predorsal bones is much more diverse in the centrolophid genus *Schedophilus*. Four patterns were encountered among species within this genus with only one pattern shared by as many as three species:

Pattern number 1:
0/0/0 + 2/ (similar to usual pattern in nomeids). Observed in *S. pemarco* and *S. haedrichi.*
Pattern number 2:
0/0 + 0/2 + 1/ observed in *S. maculatus* and *S. griseolineatus.*
Variant of pattern number 2:
0/0 + 0/1 + 1 + 1/ or 0/0 + 0/1 + 1 + 1 + 1/. Observed in *S. medusophagus.*
Pattern number 3:
0/0/2 + 1 + 1/ or 0/0/2 + 1 + 1 + 1/. Observed in *S. ovalis* and *S. labyrinthicus.*
Pattern number 4:
0 + 0/1 + 1 + 1/ or 0 + 0/1 + 1/. Observed in *S. huttoni.*

The pattern observed in *Seriolella violacea* and *S. porosa* was the same as pattern number 1 above, i.e., 0/0/0 + 2/. This same pattern was developed in *Psenopsis anomala* and *Hyperoglyphe bythites*.

Icichthys lockingtoni has an exceptionally high predorsal count for a perciform fish, usually 7 to 11 (occasionally 12), alternatively spaced with neural spines in a one to one relationship. A predorsal precedes the first neural spine and the first pterygiophore supports one dorsal spine in a secondary association.

Among radiographs loaned to us by Dr.

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[1] In this formula, each 0 represents a predorsal, each slant a neural spine, and the numerals indicate the number of spines (or rays) borne by the first and subsequent pterygiophores in a secondary association.

Haedrich is one of *Tubbia tasmanica* in which the arrangement of predorsal bones and the anterior dorsal pterygiophore is similar to *Nomeus*, i.e., 0/0/0 + 1/. *Tubbia* almost certainly is a distinct monotypic genus in the family Centrolophidae, perhaps most closely allied to *Schedophilus*. The predorsal pattern observed in *Centrolophus niger* is 0/0/0/1 + 1/, a variant of the pattern in *Cubiceps gracilis* and *C. capensis*.

Amarsipus has only three predorsal bones, with the first spaced between the first and second neural spines. The following two arrangements have been noted in *Amarsipus*:

Usual: /0/0/0///1 + 1/ or
Occasional: /0/0//0//1 + 1/.

No predorsal bones were observed in *Tetragonurus*, although this character was carefully checked on radiographs and cleared and stained specimens of the three species. The first dorsal pterygiophore carries but a single spine in a secondary association. This pterygiophore usually follows the fifth neural spine in *T. pacificus*, the sixth neural spine in *T. atlanticus*, and seventh or eighth neural spine in *T. cuvieri*.

Caudal Fin Complex

By caudal fin complex we simply refer to the caudal fin and its supporting bones. The stromateoid caudal fin has 17 principal caudal rays and a variable number of secondary caudal rays. The principal rays are divided into two lobes, the superior with nine rays (eight branched), and the inferior with eight rays (seven branched). For the 19 species dealt with by us, the range in number of secondary rays is from seven to 15 per side, with counts of the two sides (dorsal and ventral) either the same or differing usually by only one ray. For any given species the range in secondary ray counts per side is usually three, occasionally four (Table 1 and 5). Secondary ray counts were instrumental in directing our attention to two species of *Cubiceps* (called by us *Cubiceps* sp. A and *Cubiceps* sp. B).

The stromateoid caudal fin has a single ural centrum, two to six hypural bones,[2] two or three epurals, and two pairs of uroneurals. All of these bones can be grouped under the blanket term of ural bones. The ural centrum forms from a single center of ossification; there is no recapitulation of previous fusions of ural centra, such as occurs in the myctophiform family Myctophidae (Moser and Ahlstrom, 1970).

Arrangements of ural bones are usually shared by all members of a family. Members of the family Centrolophidae retain the primitive complement of three superior and three inferior hypurals. In the family Nomeidae, adults have two superior and two inferior hypurals, but during larval development the fusion from 3 + 3 hypural bones is recapitulated. Tetragonurids also have only 2 + 2 hypurals. Although not included in Table 5, we have examined specimens of several species of *Ariomma* and all have the hypurals of each lobe fused into a single plate (1 + 1), as previously reported by Haedrich (1967). Most stromateoid fishes retain the primitive complement of three epurals; the number of epurals is reduced to two in *Tetragonurus* and *Icichthys*. Two pairs of uroneurals were present in all species studied.

The vertebra immediately adjacent to the ural centrum has the neural spine markedly reduced, a condition found in perciform fishes in general. The haemal spine on this vertebra is autogenous, as is also that on the vertebra immediately forward. The presence of two autogenous haemal spines on the two vertebrae adjacent to the ural also is widespread among perciform fishes. However, *Icichthys* normally has a third autogenous haemal spine on the third vertebra anterior to the ural, a condition that is unusual.

Teeth

Dentition is one of the important characters for distinguishing among species and

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[2] In the counts of hypurals, the parhypural is not separately discriminated, but rather it is counted as an inferior hypural.

Table 5. Counts of the stromateoid caudal fin and supporting bones

Families/Species	Principal caudal rays	Secondary caudal rays d	Secondary caudal rays v	Hypurals* Sup. Inf.	Epurals	Uro-neurals	Autogenous haemal spines	Ural centra
Amarsipidae								
Amarsipus carlsbergi	9+8	11-15	11-14	3+3	3	2	2	1
Centrolophidae								
Icichthys lockingtoni	9+8	11-13	10-13	3+3	2-(3)	2	2-3	1
Schedophilus huttoni	9+8	10-12	9-11	3+3	3	2	2	1
Schedophilus labyrinthicus	9+8	11	10	3+3	3	2	2	1
Schedophilus maculatus	9+8	10-11	10	3+3	3	2	2	1
Tetragonuridae								
Tetragonurus atlanticus	9+8	9-10	9-10	2+2	2	2	2	1
Tetragonurus cuvieri	9+8	9-13	9-12	2+2	2	2	2	1
Tetragonurus pacificus	9+8	11	11	2+2	2	2	2	1
Nomeidae								
Nomeus gronovii	9+8	8-9	8-9	2+2	3	2	2	1
Cubiceps caeruleus	9+8	7-10	7-10	2+2	3	2	2	1
Cubiceps capensis	9+8	8-10	8-10	2+2	3	2	2	1
Cubiceps gracilis	9+8	8-10	8-10	2+2	3	2	2	1
Cubiceps pauciradiatus	9+8	8-10	8-10	2+2	3	2	2	1
Cubiceps squamiceps	9+8	8- 9	8- 9	2+2	3	2	2	1
Cubiceps sp. A	9+8	12-13	12	2+2	3	2	2	1
Cubiceps sp. B	9+8	11-12	12	2+2	3	2	2	1
Psenes arafurensis	9+8	7-10	7-10	2+2	3	2	2	1
Psenes cyanophrys	9+8	7- 9	7- 9	2+2	3	2	2	1
Psenes maculatus	9+8	8	8- 9	2+2	3	2	2	1
Psenes pellucidus	9+8	8-10	8-10	2+2	3	2	2	1
Psenes sio	9+8	7-10	8-10	2+2	3	2	2	1

* Parhypural counted as an hypural

genera of stromateoid fishes (Haedrich, 1972). In Table 6 we are characterizing the kinds of teeth developed on the upper and lower jaws, as well as those on the vomer, palatine, and tongue (glossohyal) for 12 of the eastern Pacific species. The characteristic teeth form during the juvenile period, sometimes over a considerable size range.

The teeth of the upper jaw (premaxillary teeth) are uniserial, conical, tapering, often moderately recurved and usually of several sizes. Although upper jaw teeth do differ somewhat among stromateoid fishes, differences are negligible when compared to the kinds of teeth on other jaw bones.

There are basically two types of teeth in the lower jaw. Many stromateoid fishes have dentary teeth that are similar to upper jaw teeth, i.e., they are conical, tapering, usually recurved and often of several sizes. However, the three species of *Tetragonurus* and four of the five species of *Psenes* have blade-like dentary teeth. These teeth are of uniform width over most of the blade, then abruptly taper to a point posteriorly. The size of specimens on which these blade-like teeth develop is discussed below for *P. sio*.

Teeth are developed on the vomer in all species included in Table 6 except *Icichthys lockingtoni*. However, for the five species of *Psenes* and for *Amarsipus* and *Nomeus*, teeth are limited to a patch on the head of the vomer, whereas teeth are developed on the blade of the vomer in *Cubiceps* and *Tetragonurus*. These teeth on the blade of the vomer can be used to separate *Cubiceps caeruleus* from the following species of *Cubiceps*. In *C. caeruleus* the teeth on the blade are conical and occur in a single, longitudinal row, whereas in *C. pauciradiatus* and *C. capensis*, the teeth are knob-like and occur in a broad patch on the blade. Tongue teeth are similar to vomerine teeth in these three species of *Cubiceps*, occurring

Table 6. Dentition of juveniles and adults of pelagic stromateoid fishes

Species	Premaxillary teeth		Dentary teeth		Palatine	Vomer	Tongue (glossohyal)
Amarsipus carlsbergi	uniserial	conical	uniserial	conical	absent	small patch on head of vomer	absent
Icichthys lockingtoni	uniserial	conical	uniserial	conical	absent	absent	absent
Tetragonurus cuvieri	uniserial	conical	uniserial	blade-like larger than upper jaw teeth	single row	longitudinal row on blade	present
Nomeus gronovii	uniserial	conical	uniserial	conical	single row	short row near head of vomer	absent
Cubiceps caeruleus	uniserial fine, recurved	conical	uniserial	conical	single row	single row on blade	single row
Cubiceps capensis	uniserial	conical	uniserial	conical	single row	knobby patches on blade	knobby patch
Cubiceps pauciradiatus	uniserial	conical	uniserial	conical	single row	broad patch	oval knobby patch
Psenes arafurensis	uniserial	conical	uniserial	mostly blade-like	single row	patch on head of vomer	absent
Psenes cyanophrys	uniserial	conical	uniserial	conical	single row	same	absent
Psenes maculatus	uniserial	conical	uniserial	mostly blade-like	single row	same	absent
Psenes pellucidus	uniserial	conical	uniserial	mostly blade-like	single row	same	absent
Psenes sio	uniserial	conical	uniserial	mostly blade-like	single row	same	absent

in a single row in *C. caeruleus* and in knobby patches in the other two species. Tongue teeth are absent in *Psenes*, *Nomeus*, *Icichthys*, and *Amarsipus*. Palatine teeth are developed in a single row per side in the three genera of nomeids and in *Tetragonurus*, but are absent in *Icichthys* and *Amarsipus*.

The striking difference between the dentary teeth and those on the premaxillary of *Tetragonurus* and most *Psenes* are not to be seen in larvae, but form during the early juvenile period. The sequence of formation can be exemplified by using *Psenes sio* as an example. None of the blade-like teeth in the lower jaw are present on a 9.0-mm larva which has only four premaxillary and three dentary teeth per side, all small. A 13.4-mm specimen (an early juvenile) has eight premaxillary and seven dentary teeth per side, but only one of the latter is broad-based and knife-like. However, the difference between the size and shape of teeth in the two jaws is marked in the 22.5-mm juvenile. This specimen has 10 premaxillary teeth and 15 dentary teeth per side. The teeth in the upper jaw are rather small, narrow, pointed, recurved posteriorly, and irregularly spaced, although uniserial. The teeth in the lower jaw, also aligned uniserially, are markedly larger, especially the sixth to the 11th, and these are blade-like, much as in *Tetragonurus*. The anterior dentary teeth are less wide and more tapered, with one or two teeth per side that could be classed as canines. The posterior dentary teeth are shorter than the teeth in the middle but equally wide-based and blade-like.

Similary, the development of glossohyal teeth on the tongue was followed for *Cubiceps pauciradiatus*. In a 30-mm specimen, a single sharp tooth is present on the posterior end of the glossohyal. Teeth are added in a single series anteriorly until about 55 mm. Knob-like teeth are then added laterally so that by about 65 mm the patch is three teeth wide, and by 100 mm, the patch is 10 to 12 teeth wide and fairly large. A similar development is taking place on the blade of the vomer, where a large oval patch of knob-like teeth is developed by 100 mm.

Eggs of Pelagic Stromateoid Fishes

Our studies of early life history stages of pelagic stromateoid fishes primarily have been concerned with their larvae and juveniles, not their eggs. However, eggs are definitely known for six species and tenta-

Table 7. Localities of capture and sizes of eggs of pelagic stromateoid fishes

Species	Station	Latitude	Longitude	Date	No. eggs	Egg diameter		Oil globule diameter	
						Ave. (mm)	Range (mm)	Ave. (mm)	Range (mm)
Centrolophidae									
Icichthys lockingtoni	G6401-76.63	34°45.0'N	121°54.0'W	I.22.64	28	1.69	1.60-1.78	0.39	0.36-0.40
" "	G6401-76.70	34°32.0'N	122°21.0'W	I.21.64	20	1.68	1.58-1.78	0.37	0.30-0.40
" "	G6401-79.74	33°48.5'N	122°13.0'W	I.17.64	15	1.67	1.52-1.80	0.38	0.30-0.40
" "	G6401-81.67	33°46.5'N	121°30.5'W	I.14.64	24	1.67	1.56-1.76	0.40	0.34-0.44
Tetragonuridae									
Tetragonurus cuvieri	Norpac 21	42°18.0'N	135°19.0'W	VIII.18.55	10	1.17	1.10-1.24	ca.0.25	-
" "	" 41	38°39.0'N	142°59.0'W	VIII.16.55	3	1.18	1.16-1.22	ca.0.25	-
" "	" 43	38°35.0'N	149°59.0'W	VIII.25.55	4	1.19	1.12-1.26	ca.0.25	-
" "	" 67	33°04.0'N	128°45.0'W	IX.3.55	25	1.21	1.12-1.28	ca.0.25	-
" "	" 96	29°41.0'N	120°43.5'W	IX.16.55	5	1.17	1.12-1.22	ca.0.25	-
" "	" 110	28°56.0'N	117°38.0'W	IX.20.55	25	1.17	1.10-1.27	ca.0.25	-
" "	C5504-103.70	29°44.5'N	119°05.0'W	IV.21.55	18	1.15	1.12-1.18	0.28	0.25-0.30
" "	C5504-103.80	29°26.0'N	119°44.5'W	IV.20.55	10	1.19	1.12-1.26	0.28	0.25-0.30
Nomeidae									
Cubiceps pauciradiatus	ETP 12.071	05°47.5'N	104°58.0'W	II.24.67	9	0.75	0.74-0.78	0.19	0.16-0.20
" "	ETP 12.077	04°06.0'N	105°00.0'W	II.25.67	37	0.75	0.70-0.78	0.18	0.16-0.20
" "	ETP 12.079	03°31.2'N	105°02.0'W	II.25.67	38	0.75	0.70-0.80	0.19	0.16-0.20
" "	ETP 12.206	03°40.0'S	112°07.0'W	III.12.67	6	0.76	0.74-0.80	0.18	0.16-0.18
" "	ETP 45.035	14°11.2'N	119°03.8'W	VIII.10.67	10	0.74	0.72-0.76	0.17	0.16-0.18
" "	ETP 45.313	04°55.0'N	111°53.5'W	IX.4.67	8	0.75	0.72-0.78	0.17	0.16-0.18
" "	ETP 45.343	13°56.3'N	110°34.0'W	IX.8.67	33	0.73	0.70-0.76	0.16	0.14-0.18
" "	ETP 45.344	14°12.5'N	110°23.0'W	IX.8.67	6	0.74	0.72-0.76	0.18	0.16-0.20
Cubiceps caeruleus	ETP 60.068	01°29.0'N	118°43.0'W	XII.29.67	20	0.91	0.84-0.92	0.21	0.16-0.22
" "	ETP 60.090	02°35.0'S	118°45.0'W	XII.31.67	5	0.90	0.88-0.92	0.20	0.20-0.22
" "	ETP 60.092	02°58.0'S	118°46.0'W	XII.31.67	14	0.92	0.90-0.94	0.21	0.16-0.22
" "	ETP 60.095	02°20.0'S	111°48.0'W	I.2.68	4	0.93	0.88-0.96	0.21	0.20-0.22
" "	ETP 75.060	01°25.0'N	118°58.0'W	II.25.68	18	0.91	0.88-0.94	0.20	0.20-0.22
Psenes sp.	ETP 11.148	11°24.5'S	118°56.2'W	II.11.67	10	1.00	0.98-1.04	0.23	0.22-0.24
(prob. arafurensis)	ETP 11.084	02°27.0'N	119°00.5'W	II.5.67	1	1.04	-	0.26	-
" "	ETP 45.090	00°57.2'N	119°04.5'W	VIII.16.67	4	0.98	0.96-0.98	0.24	0.22-0.24
Psenes sio	ETP 13.322	11°47.0'N	95°08.0'W	III.18.67	15	1.10	1.08-1.12	0.24	0.20-0.26
" "	ETP 46.132	15°38.0'N	98°01.0'W	IX.6.67	4	1.06	1.06-1.08	0.23	0.22-0.24
" "	ETP 46.135	12°40.0'N	92°03.0'W	IX.15.67	10	1.07	1.02-1.12	0.24	0.22-0.24
" "	ETP 46.137	11°48.0'N	92°03.0'W	IX.15.67	5	1.09	1.08-1.10	0.24	0.24-0.26
" "	ETP 46.141	10°19.2'N	91°54.0'W	IX.16.67	5	1.08	1.04-1.14	0.24	0.22-0.24
Psenes sp.	ETP 47.065	01°46.0'S	81°58.0'W	VIII.6.67	21	1.21	1.14-1.26	0.25	0.24-0.26
(prob. pellucidus)	ETP 47.173	07°54.8'S	85°06.0'W	VIII.22.67	15	1.22	1.14-1.28	0.26	0.24-0.28
	ETP 60.084	01°29.0'S	118°40.0'W	XII.30.67	1	1.22	-	0.30	-

tively identified for two additional species. The former include *Icichthys lockingtoni*, *Tetragonurus cuvieri*, *T. atlanticus*, *Psenes sio*, *Cubiceps pauciradiatus*, and *C. caeruleus*; eggs tentatively identified are those of *P. arafurensis* and *P. pellucidus* (Table 7). The eggs of five species are illustrated in Figure 2.

The eggs have a number of characters in common. They are pelagic, separate and round. The size range of egg diameters of the above eight species is from 0.70 to 1.80 mm. The outer shell of all species is unsculptured, although the shell usually is colored. The yolk is unsegmented and the perivitelline space is moderate. All eight species have a single oil globule. In middle and late stage eggs, pigment forms on the embryo and on the oil globule, but usually not on the yolk. The oil globule is positioned in the posterior part of the yolk-sac in late stage embryos and yolk-sac larvae.

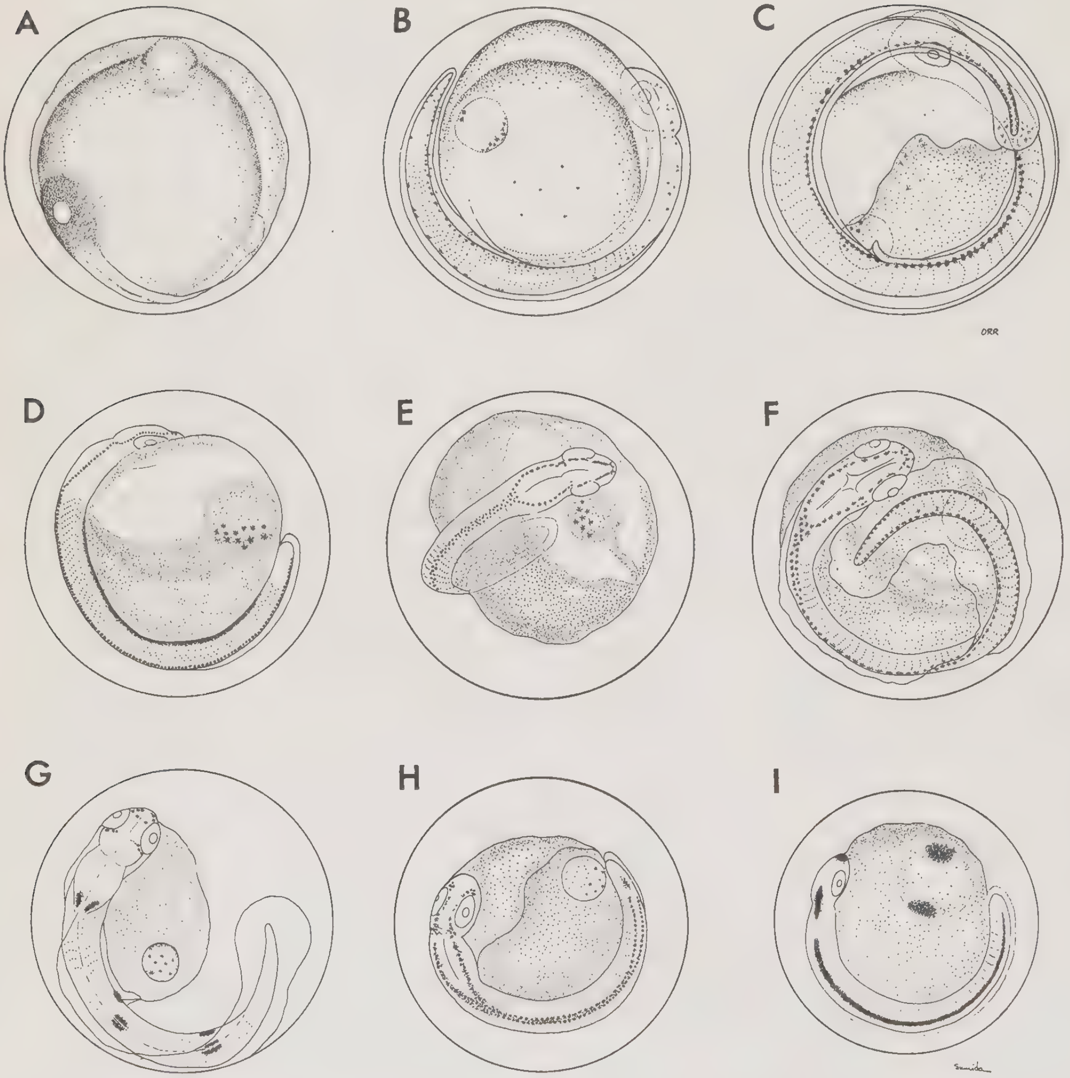

Figure 2. A-C, Eggs of *Icichthys lockingtoni*: A, early stage; B, middle stage; C, late stage. D-F, *Tetragonurus cuvieri*: D, lateral view of middle stage; E, dorsal view of middle stage; F, late stage, 1.24-mm egg diameter. G, *Psenes sio*, late stage, 1.08-mm egg diameter; H, *Psenes arafurensis*, middle stage, 0.98-mm egg diameter; I, *Cubiceps pauciradiatus*, middle stage, 0.76-mm egg diameter.

Eggs of *Icichthys lockingtoni*
Figure 2, A-C

Icichthys eggs are among the largest of pelagic stromateoid eggs in the eastern Pacific, ranging in diameter from 1.52 to 1.80 mm and in average diameter per sample between 1.67 and 1.69 mm. The oil globule also is large, ranging between 0.30 to 0.44 mm in diameter with an average diameter of 0.37 to 0.40 mm. The egg shell is not colored.

Eyes are outlined before blastopore closure. Soon after blastopore closure, anterior somites are formed. Pigment develops soon thereafter on middle stage eggs. Dorsal pigment on the embryo is scattered, rather than arranged in a double line, as in *Tetragonurus*, and although distributed on the back from the head to near the tip of tail, it is also distributed on the sides of the embryo and out over the yolk mass. Pigment is also present on the under side of the oil globule. In late stage eggs, embryonic pigment becomes concentrated along the ventral body margin from the head to the tip of tail—distributed above the digestive tract until its terminus and then along the ventral midline of the tail; dorsal pigment is scattered and sparse, but distributed along the length of the back. Pigment on the yolk becomes inconspicuous, except the patch under the oil globule which is retained.

The late stage embryo is thin bodied with a high myomere count (58 to 61), a gut length of over 50% body length, and a wide fin fold. This stage is similar to that of *Tetragonurus cuvieri* but differs in the distribution of dorsal pigment and in its higher myomere count (58 to 61 vs. 51 to 54).

Eggs of *Tetragonurus cuvieri*
Figure 2, D-F

Based on eggs from eight samples, the range in diameters of *Tetragonurus cuvieri* eggs is from 1.10 to 1.28 mm with an average diameter per sample of 1.15 to 1.21 mm; the oil globule is between 0.25 to 0.30 mm in diameter (often amorphous and hard to measure). The egg shell is golden, with a touch of pink.

Eyes form before blastophore closure. Myomeres are evident on early middle-stage eggs and pigment forms on the developing embryo soon thereafter. Initial pigment is scattered on the head but is continuous along the length of the back in a double line. By the time the tail begins to separate from the yolk (early late-stage eggs), a continuous line of ventral pigment is evident above the digestive tract and continues along the ventral margin of the free tail (Fig. 2D). Pigment on the head outlines the brain lobes and extends forward to the snout (Fig. 2E, F). During most of the late-stage period, there are continuous lines of dorsal and ventral pigment from head to tail, but before hatching most of the dorsal pigment begins to migrate ventrally except that on the very posterior part of the tail. In some late-stage embryos, there remains a concentration of pigment on the snout.

Egg of *Tetragonurus atlanticus*
(not illustrated)

A late-stage egg, unmistakably of *Tetragonurus*, was taken at EASTROPAC 11.134 located at 07°02.4′S, 118°59.0′W (February 9, 1967). The embryo has the characteristic heavy ventral pigment extending from just behind the head to the tip of the notochord, situated above the digestive tract anterior to the anus and along the ventral midline of the tail posterior to the anus. Dorsal pigment consists of a short, posterior streak ending before the terminal myomere. The only pigment remaining on the head is a patch at the snout. The egg is 1.10 mm in diameter, with a 0.24-mm diameter oil globule. Of the two tropical species of *Tetragonurus*, *T. atlanticus*, and *T. pacificus*, this egg obviously belongs to the former. It has the basic pigment pattern that is seen on small, preflexion larvae of *T. atlanticus*. The egg shell is colored like those of *T. cuvieri*.

Eggs of *Cubiceps pauciradiatus*
Figure 2, I

Eggs of *C. pauciradiatus* were observed in a number of samples. Measurements were made on eggs from eight samples. This is the smallest stromateoid egg encountered. Range in egg diameter is from 0.70 to 0.80 mm, with an average diameter of 0.75 mm; the oil globule is smaller than in other stromateoid eggs, ranging in diameter from 0.14 to 0.20 mm, with an average of 0.18 mm. The outer shell is lightly colored a pinkish tan.

The late-stage embryo is conspicuously

pigmented. The principal pigment is a wide, dark band of pigment extending along the back from behind the head to near the tip of the notochord. Initially, this is a double, separated line of pigment down the back, but pigment soon fills in between the lines. The most characteristic pigment on the late-stage embryo, however, is the patch that forms on the tip of the snout. This snout pigment is a character that simplifies recognition (identification) of these eggs. Between the snout and the nape there is a median group of pigment spots on the head. The oil globule is characteristically pigmented, having two opposing patches of pigment. In most stromateoid eggs, the dorsal pigment is rearranged on late-stage embryos, often approaching the pattern to be found on yolk-sac larvae. Such rearrangement of pigment apparently does not occur in late-stage eggs of *C. pauciradiatus*, as we observed no eggs in which any pigment had moved ventrally. A similar situation is noted for *C. caeruleus*, which retains the dorsal pattern of pigmentation without rearrangement on late-stage eggs.

Eggs of *Cubiceps caeruleus*

(not illustrated)

Eggs of *C. caeruleus* are 0.84 to 0.96 mm in diameter (average 0.91) with an oil globule 0.16 to 0.22 mm in diameter (average 0.20). The egg shell is light tan in color.

This egg is larger than that of *C. pauciradiatus* and the embryo is somewhat differently pigmented. Both have a band of pigment extending along the length of the back, but head pigment is quite differently arranged. Pigment is lacking on the center of the head in *C. caeruleus* but instead outlines the brain lobes and extends forward between the margin of the eyes to the snout. It is quite similar to head pigment on late-stage embryos of *Tetragonurus*. Even on late-stage eggs, the dorsal pigment remains as a solid band without rearrangement and no ventral pigment was observed; hence, in these characters, eggs of *Cubiceps caeruleus* parallel the pigment pattern observed on eggs of *C. pauciradiatus*. The oil globule is pigmented on its outer margin, away from the embryo.

Eggs of *Psenes sio*

Figure 2, G

Eggs of this species were seen in a number of samples from the eastern tropical Pacific. Range in egg size, based on five samples, is 1.02 to 1.14 mm, and average diameter is 1.09 mm; oil globules range between 0.20 to 0.26 mm in diameter, averaging 0.24 mm. The egg shell has a pinkish straw color.

On an early-stage egg, just prior to blastopore closure, the embryo is outlined as a rod, without eyes, separation of somites, or pigmentation. On an early middle-stage egg eyes are outlined, about 12 somites can be counted in back of the head, and pigment is present on the head and in a double row dorsally on the body. By the end of this stage, the pigment moves ventrally but is still evident along the length of the embryo. Pigment also is present completely around the oil globule. On late-stage embryos, pigment is sparse on top of the head but outlines the brain lobes posteriorly and is heavy on the underside of the head. Body pigment becomes concentrated into three areas: first, a lateral pigment dash and a corresponding ventral patch above the gut a few somites behind the head; second, a ventral patch above the gut near its termination, and an associated dorsal patch above and slightly posterior to the anus; third, midway along the tail, there are opposing dorsal and ventral pigment patches. The pigment on late-stage embryos corresponds to that found on yolk-sac larvae.

Eggs of *Psenes pellucidus*

(Tentative Identification)

(not illustrated)

Eggs tentatively identified as *P. pellucidus* are strikingly similar to those of *P. sio*, but larger in size and with more heavily pigmented shells. Egg diameters range from

1.14 to 1.28 mm (average 1.21 mm); oil globule diameters range from 0.24 to 0.28 mm (average 0.26 mm). The outer egg shell is brownish with a tinge of rose. The pigment pattern on late-stage embryos is similar to that described above for *P. sio*, including heavy pigment on the underside of the head, on the snout, and on the back of the head, as well as its concentrations into three areas along the body. A late-stage egg, taken offshore, has added an additional pigment area on the posterior part of the tail, but otherwise, is similarly pigmented. The number of somites (ca. 40) on the embryo is too high for *P. arafurensis* or *P. cyanophrys*. These larger-sized *Psenes* eggs were taken only in the three samples listed in Table 7, in contrast to *Psenes sio* eggs which were observed in more than 50 samples. The heavy pigment under the head on late-stage embryos undoubtedly is the source of the striking pigment patch that develops under the head on only the preflexion larvae of *P. sio* and *P. pellucidus*. This head pigment was one of the prime considerations in the tentative assignment of these eggs to *P. pellucidus*.

Eggs of *Psenes arafurensis*
(Tentative Identification)
Figure 2, H

Nomeid eggs, 0.96 to 1.04 mm in diameter, with an oil globule 0.22 to 0.24 mm in diameter were taken in several offshore stations. The pigment pattern described below is based on the egg farthest along in development, taken at station ETP 11.084. On the head region of the embryo, pigment outlines the brain lobes and extends forward to the snout—the usual pattern in stromateoid eggs. On the back, a band of pigment extends along the trunk and on the forward portion of the tail; behind this on the tail the pigment is clustered into two dorsal patches with some lateral and ventral melanophores below each patch.

Just behind the head the pigment is moving laterally into the area where the anterior-most of the patches of body pigment are present on late-stage eggs of *P. sio* and *P. pellucidus*. Ventral pigment also is present above the gut near its termination, the area of the second body pigment patch on larvae of the above two species. Hence, the pigment arrangement on late-stage eggs is intermediate between that found on eggs of *Cubiceps* in which the dorsal pigment remains intact during embryonic development prior to hatching, and in *P. sio*, in which embryonic pigment rearranges before hatching to the pattern encountered on early preflexion-stage larvae. The eggs are only lightly colored a pale straw color. The oil globule has melanophores on its outer margin. The egg illustrated is not as far advanced as the late-stage egg described above, and only the posterior-most patch is separated from the dorsal band on the body of the embryo. The eggs were obtained in an area where larvae and juveniles of *P. arafurensis* also were obtained. We are reasonably certain that the eggs are those of *P. arafurensis*.

Family AMARSIPIDAE

This is a monotypic family; *Amarsipus carlsbergi* is the only stromateoid fish that lacks toothed pharyngeal sacs. The species has a mixture of primitive and more specialized characters. The supporting bones of the caudal fin include three superior hypurals and three inferior hypurals (parahypural included) and usually three epurals; this is the primitive complement for perciform fishes and is a character shared with centrolophids, but not with other stromateoid fishes (Table 5). However, the more advanced number of only six branchiostegal rays is present, whereas centrolophids still retain seven.

Genus *Amarsipus*

The slender body of juveniles is compressed and flabby with translucent areas along the body adjacent to the dorsal and anal fins. The two dorsal fins are barely separated; the spines in the first dorsal are

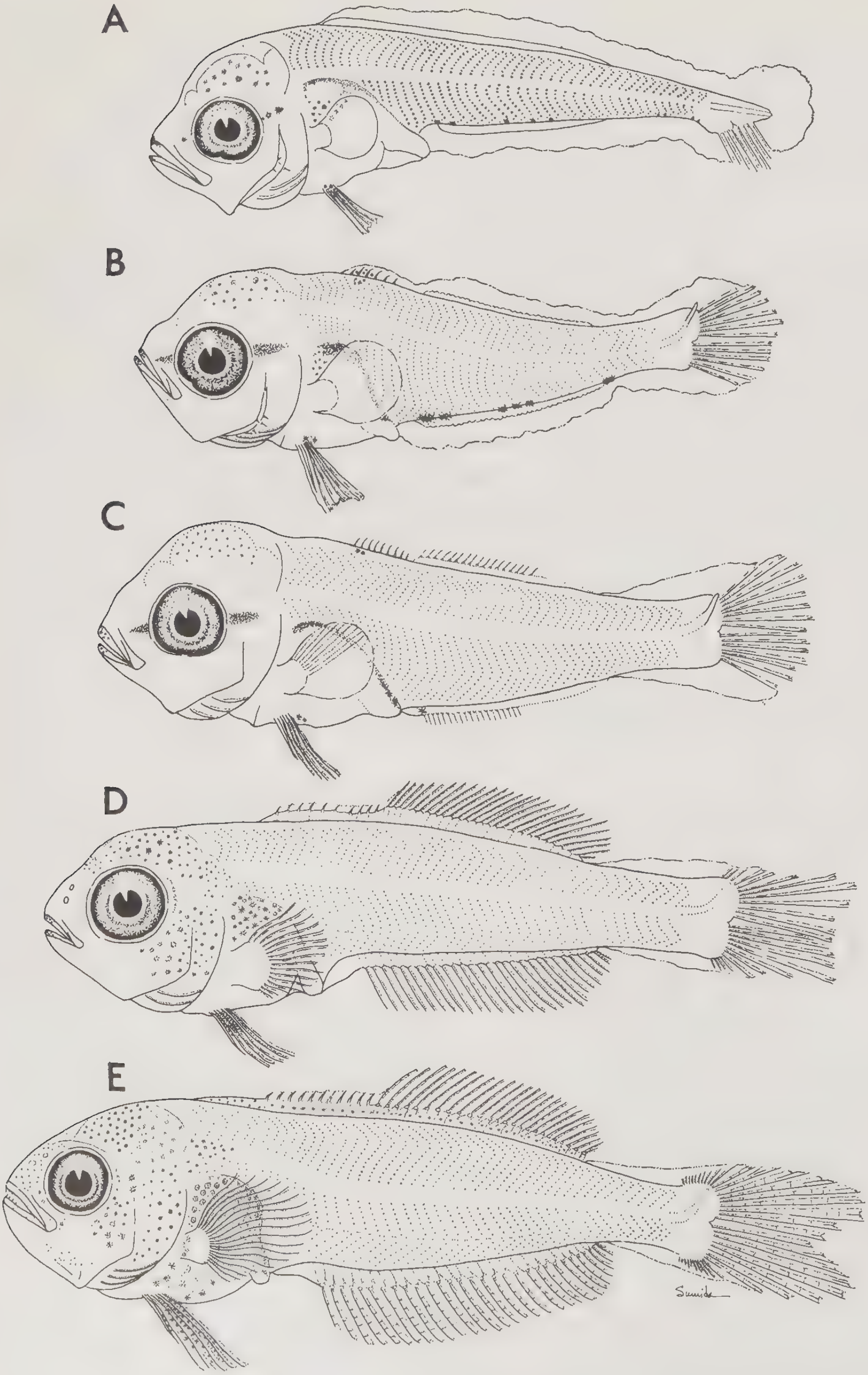

Figure 3. Developmental stages of *Amarsipus carlsbergi* (Amarsipidae). A—5.7-mm early flexion larva; B—4.6-mm late flexion larva; C—6.0-mm late flexion larva; D—11.5-mm postflexion larva; E—16.7-mm postflexion larva.

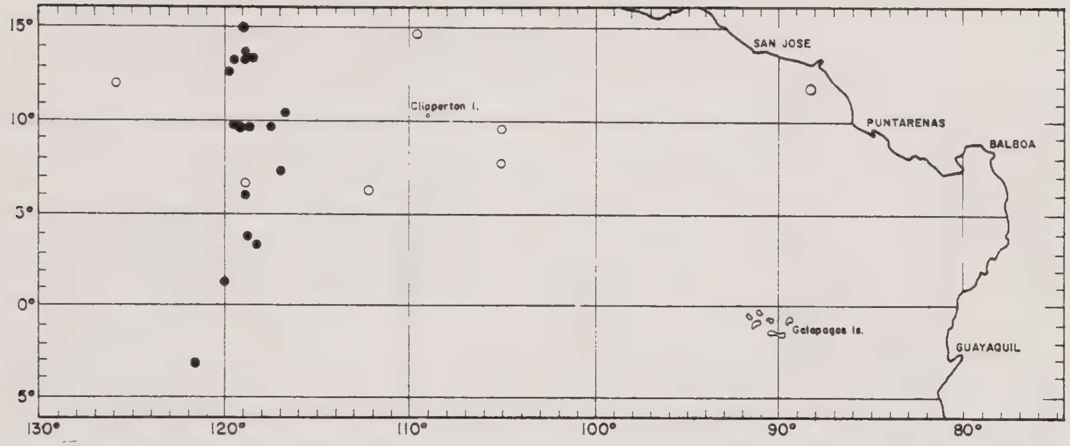

Figure 4. Occurrences of *Amarsipus carlsbergi* larvae (open circles) and juveniles (closed circles) in the eastern tropical Pacific.

quite short but the rays in the second dorsal are relatively long. The arrangement of spines and rays in this fin most closely resembles that of *Tetragonurus*. However, the number of soft rays in the second dorsal and anal fin of *Amarsipus* is at least twice the number found in *Tetragonurus*. The caudal peduncle is broad and relatively long. The pelvic fins are jugular in juveniles, but on early stage larvae they form behind the pectoral base. The vertebral count of (45) 46 to 48, is in the range of that of *Tetragonurus*, lower than for *Icichthys*, but higher than for other stromateoid fishes. The dorsal fin is farther back on the body than in most stromateoids—the origin of the fin follows the 6th neural spine. The first dorsal pterygiophore supports a single spine in a secondary association, a character shared with several centrolophids (*Centrolophus niger*, *Schedophilus medusophagus*, *S. huttoni*) and with *Nomeus gronovii*, but still is unusual, inasmuch as in other stromateoid fishes the first dorsal pterygiophore supports two spines in a secondary association. The arrangement of the three predorsal bones in relation to neural spines is unique among stromateoid fishes (refer to section titled "Predorsal Bones"). The largest known specimen, 124 mm, is probably still a juvenile. Hence the size attained by adults is not known.

Amarsipus carlsbergi Haedrich, 1969
Figure 3

Literature.—Haedrich (1969), in the original description of the monotypic family Amarsipidae, recorded three specimens of the new species, *Amarsipus carlsbergi* from the eastern Pacific. Ahlstrom (1972) reported catch localities of seven specimens from EASTROPAC cruises, ranging in length from 7.2 to 30.0 mm.

Material.—Sixteen collections of juveniles and eight collections of larvae were studied. The biggest specimen (124 mm) is the largest yet reported; however, it appears to us to be a juvenile.

Distribution.—*A. carlsbergi* was found mostly offshore in the eastern Pacific between 15°N and 5°S (Fig. 4). This species was also found near Hawaii but not to the north (Fig. 5). The species is rare in plankton collections but large midwater trawls towed near the surface collect juveniles frequently.

Distinguishing Characters.—JUVENILES. *A. carlsbergi* is unique among stromateoids in the combination of its vertebral count with the dorsal and anal fin meristics (Table 1).

LARVAE. The pelvic fins are precocious in development as is also characteristic of

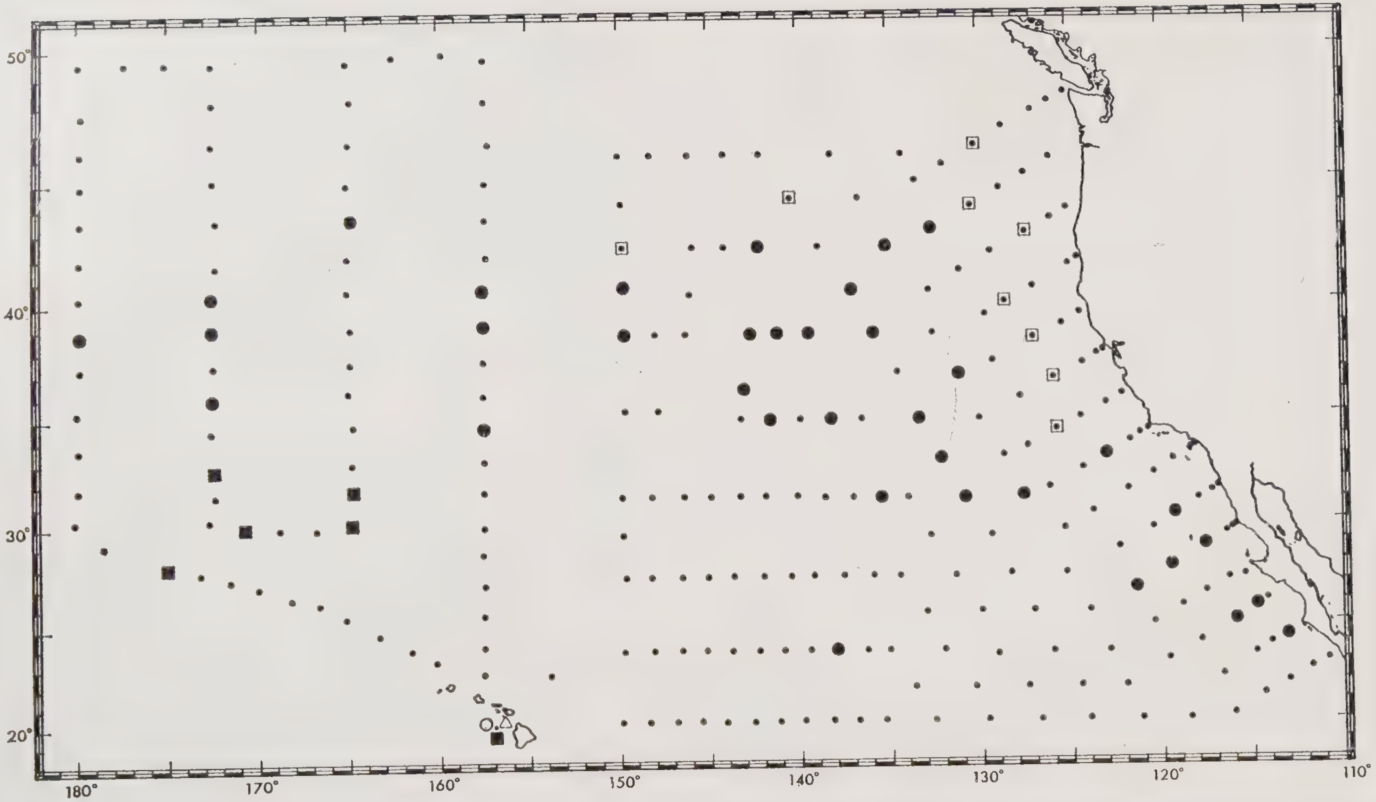

Figure 5. Location of collections of *Amarsipus carlsbergi* (open triangle), *Icichthys lockingtoni* (open square with center dot), *Tetragonurus atlanticus* (closed squares), *T. cuvieri* (closed circles), and *T. pacificus* (open circle) in the NORPAC Expedition, August-September 1955. Small dots indicate occupied stations.

Psenes and probably *Nomeus*. Small larvae have a bar of pigment through the eye like that developed in *Cubiceps caeruleus*, *Tetragonurus atlanticus*, and less strikingly in *Icichthys lockingtoni* and *T. cuvieri*. Myomere counts will distinguish *A. carlsbergi* from *C. caeruleus* and *I. lockingtoni*, and the shorter gut and the longer second dorsal and anal fins will separate it from *Tetragonurus*. Pigmentation on *Amarsipus* larvae is very sparse, primarily being confined to the head and abdominal region.

Meristics.—Vertebrae 16 to 18 + 29 to 31 = 46 to 48 (average 46.6); first dorsal X to XII (average 11.0); second dorsal 23 to 27 (average 24.8); anal 29 to 32 (average 30.3); principal caudal rays 9 + 8; secondary caudal rays 11 to 15 dorsal + 11 to 14 ventral (average 12.5 + 12.4).

Meristics of 20 specimens from about 3°S to about 13°N are given in Table 8. No latitudinal variation of any count is evident.

Morphometrics.—*Amarsipus* is a relatively slender-bodied stromateoid fish, with its greatest body depth at the pectoral and tapering gradually toward the caudal peduncle. Morphometric data for a size series are presented in Table 9, and body proportions are summarized in Table 10. The head length (HL) is short relative to body length, averaging about 25% of SL (22 to 28%) on postflexion larvae and early juveniles. Eye diameter is about 40% of HL in postflexion specimens (38 to 41%). The snout, which remains bluntly pointed during larval development is 21 to 29% of HL. The body becomes more slender during development, body depth decreasing from ca. 33% of SL at flexion to ca. 23% of SL in 28- to 32-mm specimens.

The position of the pelvic fins changes markedly with growth. In the three smaller specimens, the snout to pelvic fin distance is 28% of SL, whereas, in other specimens it ranges between 19 to 21% of SL. The pelvic fins are always forward of the dorsal fin after its formation; the snout to dorsal fin origin (Sn-D) is 30 to 35% of SL as compared to 19 to 21% of SL for the pelvic fin on postflexion larvae and early juveniles. The origin of the anal fin precedes the origin of the second dorsal fin. The snout to anal fin origin (Sn-A) is 40 to 50% of SL. Despite the considerable length of the anal fin, *Amarsipus* has a well-marked caudal peduncle, intermediate in relative length between the strikingly long caudal peduncle of *Tetragonurus* and the shorter caudal peduncle on *Icichthys*.

Ossification.—Meristics from a series of eight specimens, 4.5 to 32.0 mm, are presented in Table 11. Only one specimen 21.4 mm long was cleared and stained with remaining ones kept intact for the limited collection of small-sized larvae. Although the series consists of only a few specimens, it is possible to trace the sequence of fin formation.

The pelvic fins are the first to develop rays, being formed on an early flexion specimen (Fig. 3A). *Amarsipus* shares this character of early forming pelvic fins with larvae of *Psenes* and probably *Nomeus*. Principal caudal rays are next to ossify with 7 + 6 rays present at 4.6 mm (Fig. 3B), 8 + 7 rays on 6.0-mm specimen, and the full complement of 9 + 8 principal rays on the 11.5-mm specimen. By late flexion (4.6 mm), spines are forming in the first dorsal, rays are forming in the pectoral fin, and the anlagen of the second dorsal and anal fins are present. By 6.0 mm (Fig. 3C), the first dorsal is complete and rays are ossified in the second dorsal and anal fins. No specimens are available between 6.0 and 11.5 mm; in the latter specimen (Fig. 3D), all fins are complete except for secondary caudal rays which are not fully developed until about 21.4 mm.

An account of the sequence of vertebral ossification cannot be given due to a lack of cleared and stained material. The complete set of 2 + 4 branchiostegal rays are present at 4.5 mm in addition to eight gill rakers and a few small preopercular spines. The weak, inconspicuous preopercular spines are

Table 8. Meristics of 20 juveniles of *Amarsipus carlsbergi* selected from over its distributional range in the eastern Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Jord. 57.013	13°27'N	119°01'W	XI.9.70	79.8	16+31=47	X	24	31	12-17-13
"	"	"	"	51.2	16+31=47	XII	24	32	13-17-13
"	"	"	"	46.0	16+30=46	XII	26	31	13-17-12
"	"	"	"	42.5	16+30=46	XI	25	30	12-17-12
Jord. 57.012	13°16'N	119°23'W	XI.8.70	124.0	17+29=46	XI	24	29	13-17-13
"	"	"	"	43.0		XI	27	30	12-17-12
"	"	"	"	29.0	16+31=47	XII	24	31	11-17-12
Jord. 57.018	13°16'N	118°51'W	XI.9.70	23.0	17+30=47	X	26	30	12-17-11
Jord. 57.106	13°13'N	120°12'W	XI.7.70	50.8	16+30=46	XI	24	30	13-17-13
Jord. 60.160	10°57'N	116°48.5'W	IV.9.71	43.0	16+31=47	XI	25	31	12-17-11
"	"	"	"	40.5	16+31=47	XI	25	30	12-17-12
"	"	"	"	35.0	17+30=47	XI	25	30	-
Jord. 57.030	9°43.5'N	119°30'W	XI.12.70	88.2	16+30=46	XI	25	30	13-17-13
Jord. 57.042	9°12'N	118°26'W	XI.13.70	27.7	17+30=47	XI	25	31	12-17-12
Jord. 60.134	7°05'N	117°00'W	IV.5.71	65.8	17+29=46	XI	23	29	12-17-12
Jord. 57.112	7°00'N	119°20'W	XII.6.70	24.0	17+30=47	XI	24	30	12-17-11
Jord. 60.031	3°57'N	118°58'W	III.9.71	37.0	17+30=47	XI	25	31	12-17-12
Jord. 57.087	3°44'N	118°24'W	XI.23.70	20.0	16+30=46	XI	24	31	13-17-13
T.C. 51.086	1°52'N	120°05'W	XI.19.70	46.0	17+31=46	XI	25	31	14-17-14
T.C. 51.071	3°12'S	121°27'W	XI.14.70	70.5	18+30=48	XII	24	30	11-17-12

few in number and are not present on postflexion larvae.

Teeth form on the premaxillary and dentary at about 6.0 mm, increasing in number with growth. Because only one specimen was cleared and stained, the initiation of scale formation was not determined. Haedrich (1969) reported lateral line scales on a 49-mm specimen.

Pigmentation.—Early larvae have pigment along the ventral margin of the body and develop pigment before and behind the eye. In postflexion larvae, the ventral margin pigment is lost and the head becomes uniformly pigmented.

Flexion larvae (Fig. 3A, B) have pigment on the head, over the abdomen, at the base of the pelvic fins, and along the ventral margin of the tail. In the early flexion specimen (5.7 mm) the tail pigment consists of nine unequally spaced melanophores. The head pigment consists of a scatter of melanophores over the brain, pigment at the tips of the upper and lower jaws, and a partially

Table 9. Morphometrics, in mm, of larvae and juveniles of *Amarsipus carlsbergi* (specimens above dashed line are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 50.170	4.6 NL	2.2	1.3	0.58	0.34	1.5	-	-	1.3
off Hawaii	5.7	2.4	1.3	0.56	0.34	1.4	-	-	1.6
ETP 13.105	6.0 SL	2.8	1.7	0.70	0.50	2.0	2.4	3.0	1.8
ETP 11.066	11.5	4.4	2.8	1.1	0.60	3.0	3.6	4.6	2.4
ETP 11.306	16.7	6.2	4.0	1.6	0.88	4.4	5.5	7.2	3.1
ETP 60.150	21.4 *	7.7	4.8	1.9	1.2	5.5	7.4	9.0	3.8
"	27.4 *	8.7	6.1	2.5	1.4	6.5	8.2	11.2	5.2
"	28.4 *	9.8	7.4	2.8	1.7	6.7	9.5	12.2	5.7
ETP 11.114	32.0 *	10.7	7.3	3.0	1.6	7.4	9.7	13.0	6.4

* Juvenile

Table 10. Body proportions of larvae and early juveniles of three species of *Tetragonurus*, of *Amarsipus carlsbergi*, and of *Nomeus gronovii*, expressed as percentage of standard length (SL) or head length (HL)

Species and stage	Size range (mm)	Snout to anus/SL	Head length/SL	Eye diameter/HL	Snout length/HL	Depth at P base/SL	Sn-D/SL	Sn-A/SL	Sn-V/SL
Tetragonuridae									
Tetragonurus atlanticus									
Preflexion	3.0- 5.8 NL	63-69	14-26	28-48	24-27	13-20	-	-	-
Flexion	7.3- 8.1 NL	64-69	27-30	28-31	22-29	18-23	-	66-71	33-36
Postflexion	8.5-17.2 SL*	64-71	30-35	29-34	28-29	24-28	40-42	65-71	33-37
Tetragonurus cuvieri									
Preflexion	4.2- 6.6 NL	57-64	11-23	33-50	20-28	10-18	-	-	-
Flexion	7.6-10.1 NL	56-62	24-27	29-34	25-28	18-20	-	60-64	29-33
Postflexion	11.4-17.4 SL	58-67	25-32	27-32	23-31	20-25	37-44	60-69	32-36
Tetragonurus pacificus									
Postflexion	8.9-19.5 SL	62-65	30-33	29-33	27-32	27-29	40-43	63-66	30-35
Amarsipidae									
Amarsipus carlsbergi									
Flexion	4.6- 5.7 NL	42-48	23-28	43-45	26	24-33	-	-	28
Postflexion	6.0-32.0 SL	32-38 (47)	22-28	38-41	21-29	23-33	30-35	40-50	19-21
Nomeidae									
Nomeus gronovii									
Postflexion	7.3-11.9 SL	56-59	30-34	38-44	19-25	37-41	38-40	57-61	26-34

* Postflexion specimens may include both larvae and early juveniles

developed eye bar. In the late flexion larvae (4.6 mm) the eye bar is well developed, the ventral tail pigment has become concentrated into six patches, and pigment is present between the developing spines of the first dorsal fin.

In the smallest postflexion larva (6.0 mm, Fig. 3C), the ventral tail pigment is reduced to a single spot, but the eye bar remains conspicuous. By 11.5 mm (Fig. 3D) pigment has become heavier on the head, although the eye bar has disappeared. Pigment is heavier over the abdomen, but has been lost on the body. The pigment at the base of the pelvic fin is spread over the fin. In the largest specimen illustrated (16.7 mm, Fig. 3E), pigment has become heavier over the head and abdomen; some pigment has been added behind the head on the body, and a line of melanophores has formed along the length of the dorsal fin base.

On juveniles (not illustrated) the unpaired fins are sprinkled with pigment, which is heaviest along their outer margins. The pelvic fins are conspicuously pigmented, but the pectorals are unpigmented.

Family CENTROLOPHIDAE

A centrolophid character possessed in common with other stromateoid fishes (except Amarsipidae) is the development of toothed pharyngeal sacs just posterior to the gill arches. Centrolophids have the blunt-nosed smug appearance that characterizes most stromateoid fishes (Haedrich, 1967). This is the largest family of stromateoid fishes, with probably seven genera. The commonest vertebral count is 10 + 15 = 25, found in all species of four genera and in some *Schedophilus*. The range in numbers of vertebrae in *Schedophilus* is 25 to 32 and is markedly higher in *Icichthys*, ranging between 50 to 61; the holotype of *Tubbia* has 43 vertebrae. The spines of the dorsal fin are weakly developed and graduate to the dorsal rays on the four species we will be dealing with, but can be stout and not graduated among some centrolophids, as in *Hyperoglyphe*. Predorsal bones number

Table 11. Meristics of larvae and juveniles of *Amarsipus carlsbergi* (specimen above dashed line is undergoing notochord flexion. Note: Only 21.4-mm specimen cleared and stained; vertebral counts of other specimens are myomere counts, or read from radiographs)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 50.170	4.5 NL	VI	base	base	7	I,5	0-7+6-0	16+30=46	2+4	0+1+7	0	0
ETP 13.105	6.0 SL	X	15	ca.23	10	I,5	0-8+7-0	16+30=46	2+4	1+1+7	1	1
ETP 11.066	11.5	X	26	ca 29	18	I,5	3-9+8-4	16+31=47	2+4	3+1+8	11	8
ETP 11.306	16.7	X	25	30	17	I,5	10-9+8-10	16+30=46	2+4	4+1+9	12	10
Jord. 60.150	21.4*	XII	24	I,29	18	I,5	12-9+8-13	16+30=46	2+4	5+1+10	22	16
"	27.4*	X	26	30	19	I,5	14-9+8-14	16+30=46	2+4	4+1+12	20	12
"	28.4*	XII	24	I,29	17	I,5	15-9+8-14	16+31=47	2+4	5+1+12	16	9
ETP 11.114	32.0*	X	26	31	18	I,5	12-9+8-12	16+30=46	2+4	4+1+12	ca 24	ca 12

* Juvenile

three, occasionally two, in all centrolophids except *Icichthys*. Hypural bones have the primitive complement for perciform fishes of three superior and three inferior (parhypural included). There are usually three epurals (two in *Icichthys*), two or three autogenous haemal spines on vertebrae adjacent to the terminal (ural) centrum, and two pairs of uroneurals.

In addition to the four species dealt with in this paper, Haedrich and Nielsen (1966) reported a 46-mm specimen of *Centrolophus niger* Gmelin (or *C. maoricus* Ogilby) from the stomach of *Alepisaurus* taken in the Pacific at 35°55′S, 116°53′W. Chirichigno (1973) described adult specimens of *Schedophilus haedrichi* from Chile.

Young specimens of centrolophid fishes are commonly collected under jellyfish. The nine specimens of juvenile *Schedophilus* available to us from the eastern south Pacific were dipnetted under jellyfish or *Physalia*. Various specimens of *Icichthys* were also collected in association with jellyfish.

The early life history stages of only one centrolophid have been described in detail, that of *Centrolophus niger* (= *C. pompilus* C. V.) by Sanzo (1932). Sanzo's illustrations are reproduced by Padoa (1956) together with additional illustrations of early juveniles of *C. niger* and a single illustration of a 44.0-mm specimen of *Schedophilus ovalis*. Haedrich (1966) illustrated three young specimens of centrolophids: *Icichthys lockingtoni*, ca. 17.0 mm; *Centrolophus niger*, ca. 13.0 mm; and *Schedophilus medusophagus*, ca. 18.5 mm. T. Senta in Uchida, *et al.* (1958) illustrated a 16.4-mm specimen of *Psenopsis anomala*; Shojima (1961) illustrated four specimens of *Psenopsis* sp. taken accompanying the jellyfish, *Aurelia aurita*. No information is given on meristics of the specimens. Dawson (1971) illustrated three small specimens of *Hyperoglyphe bythites*, 5.7 to 7.9 mm, and a juvenile, 54.9 mm SL.

Maul (1964) gave observations on live specimens of *Schedophilus maculatus* and *S. ovalis* collected from off Madeira and reared in aquaria. A specimen of *S. maculatus* reared for 2 months (May 1 to June 30, 1961) grew from 55 mm to 141 mm, just over 2.5 times, and increased in weight from 7 to 95 g, about 13 times. Another specimen captured in 1962 and kept for about 3 months increased in length from 75 to 280 mm SL. A specimen of *S. ovalis* captured at the same time as the smaller specimen of *S. maculatus* grew in 2 months from about 100 to 198 mm SL. These observations indicate a strikingly fast growth rate.

Icichthys lockingtoni also has a relatively rapid growth rate. A specimen, hatched at our laboratory on June 13, 1975, from eggs collected at sea and reared by Dennis Gruber, grew to a length of 93 mm SL and weight of 15.3 g by August 30, 1975.

Genus *Icichthys*

Icichthys originally was placed in a separate family and perhaps should again be separated as it is too disparate to fit in with the other genera placed in the Centrolophidae. One of the strikingly different characters is the origin of the dorsal fin in relation to the vertebral column and to the predorsal bones. In the other centrolophids, there are two or three predorsals preceding the dorsal fin; the anterior dorsal pterygiophore interdigitates between the second and third neural spines or the third and fourth neural spines, with the most frequent arrangement of this bone with predorsals being 0/0/0 + 2/. However, there are 7 to 11 (or 12) predorsals in *Icichthys lockingtoni*, with the anterior pterygiophore usually located between neural spines 11 and 12 or 12 and 13. This posteriad placement of the dorsal fin in relation to the vertebral column also is found in *Tetragonurus* and *Amarsipus*, although the former lacks predorsal bones, and the latter has but three predorsals. In other centrolophids with high numbers of dorsal fin elements, the fins are forward on the body, particularly so in *Schedophilus huttoni*, the species with the highest dorsal fin element count. Larvae of *Icichthys* are narrower bodied and have longer digestive tracts (pre-anus lengths) than other centrolophid larvae; in point of fact, they resemble larvae of *Tetragonurus* much more closely than those of other centrolophids. Parin and Permitin (1969) created a new genus *Pseudoicichthys* for *I. australis* Haedrich 1966. They recorded 9 to 10 predorsal bones for this species. Krefft (1969) and Haedrich and Horn (1972), although mentioning the new genus, retained *australis* in *Icichthys*. As mentioned in an earlier section, we would include *Tubbia* among the recognized genera of centrolophids.

Icichthys lockingtoni
Jordan and Gilbert, 1880
Figure 6

Literature.—This species was described by Jordan and Gilbert (1880) from a 6.8 inch (ca. 170 mm) specimen brought into the San Francisco fish market. A 64-mm specimen taken at Pacific Grove under jellyfish was described by Gilbert (1904) as *Schedophilus heathi*. Hobbs (1929) described specimens obtained from the gastrovascular cavity of the medusa *Phacellophora* from Monterey Bay as *Centrolophus californicus*. Myers (1950) pointed out that Hobbs' (1929) form represented the young of *Icichthys lockingtoni*. Fitch (1949) reported on a 55-mm specimen dipnetted under the jellyfish *Pelagia* off Seal Beach, southern California. Fitch (1952), Craig and Caneday (1962), Best and Smith (1965), and Berry and Perkins (1966) reported additional specimens from off California. Cowan (1938) reported a specimen from British Columbia; Abe (1963) reported 12 specimens from Sagami Bay, Japan. Haedrich (1966 and 1967) gave descriptions and additional records; a specimen approximately 17.0 mm SL was illustrated by Haedrich (1966).

Material.—Extensive collections of eggs, larvae, and early juveniles were examined from CalCOFI and NORPAC cruises including a series of specimens reared in the laboratory from eggs collected at sea off southern California. In addition, SIO's fairly extensive collection of juveniles and adults was utilized.

Distribution.—*I. lockingtoni* is common in the transitional waters of the California Current. It is found south almost to Punta Eugenia along Baja California (Fig. 7). Further north it is found offshore to 150°W in NORPAC samples (Fig. 5) and is known to extend across the Pacific to off Japan (Haedrich, 1966).

Distinguishing Characters.—JUVENILES. The species is characterized by its limp, compressed body, bluntly rounded snout, weakly developed scales on juveniles, weak dorsal and anal spines graduating to rays, the high vertebral number, and the posteriad origin of the dorsal fin, well behind the insertion of the pectoral fins.

LARVAE. Preflexion larvae of *I. lockingtoni* resemble those of *Tetragonurus cuvieri*, but differences in myomere counts (58 to 61 vs. 51 to 54) and in dorsal body pigment

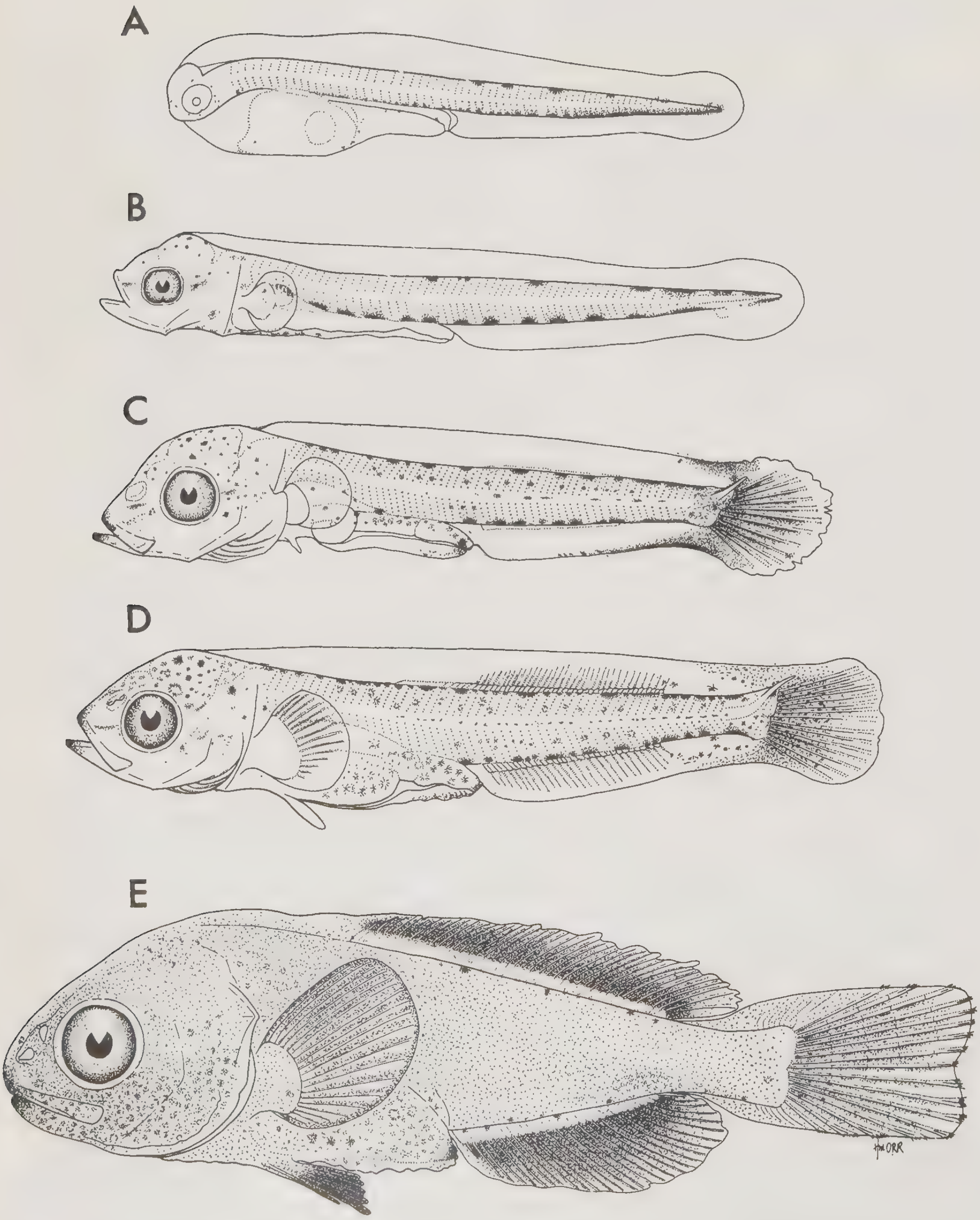

Figure 6. Developmental stages of *Icichthys lockingtoni* (Centrolophidae). A—4.3-mm preflexion larva; B—8.2-mm preflexion larva; C—10.4-mm flexion larva; D—13.5-mm postflexion larva; E—20.0-mm early juvenile.

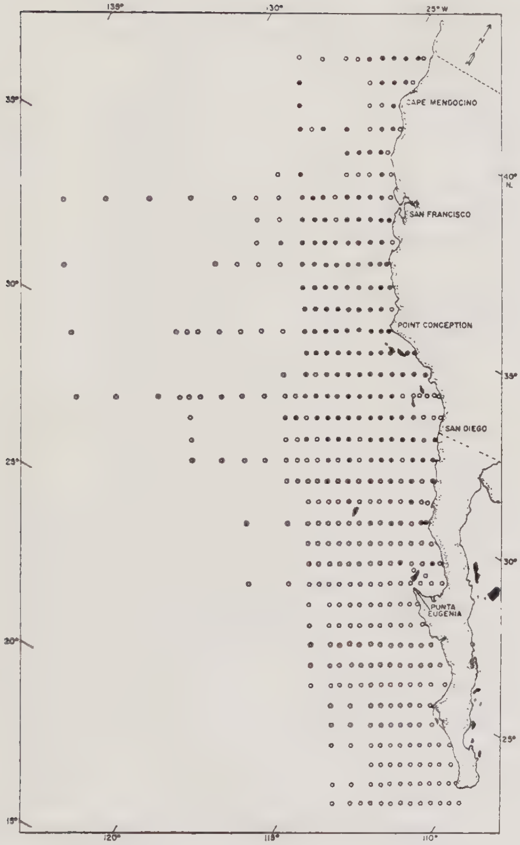

Figure 7. Distribution of *Icichthys lockingtoni* larvae in the CalCOFI region: a composite record of occurrences at CalCOFI stations during 1955-60. Closed circles are positive records, open circles are negative occurrences.

distinguish the two. *I. lockingtoni* has clusters of melanophores scattered along the posterior half of the dorsal body margin, whereas this dorsal pigment is confined to a short continuous streak on the very posterior portion of the tail in *T. cuvieri*. Once the dorsal and anal fins begin to form, there is no problem in distinguishing between the larvae of these two species (compare Fig. 6 with Fig. 13).

Meristics.—Vertebrae 23 to 25 + 34 to 37 = 58 to 61 (average 58.9); dorsal 41 to 46 (average 42.6); anal 27 to 32 (average 29.5); principal caudal rays 9 + 8; procurrent caudal rays 11 to 13 + 10 to 13 (average 12.1 + 11.9).

Meristics of 25 specimens from about 30°N to about 53°N and from about 112°W to about 173°E are given in Table 12. No variation of any count with latitude or longitude is indicated.

Morphometrics.—The morphometric measurements are given for a series of selected specimens in Table 13 and body proportions are summarized in Table 14. The early stage larvae of *Icichthys*, preflexion through flexion, are the slenderest among known stromateoid larvae, including *Tetragonurus*; body depth at pectoral fin ranges between 10 to 16% of SL. Body depth increases during the postflexion stage becoming about one-third of the standard length. The head increases in proportionate length from about 14% of NL at hatching to about 24% of NL at flexion, and to 32 to 35% of SL on late postflexion larvae and early juveniles. Eye diameter as a percentage of head length is moderately variable (29 to 41% of HL) but shows no consistent pattern of increase or decrease during larval development. After its full development on preflexion larvae, the snout retains about the same relative length (20 to 26% of HL) through the early juvenile stage. Gut length shows little proportionate variation during larval development (50 to 58% of NL or SL). Origin of the dorsal fin is somewhat forward of midbody (42 to 48% of SL). Origin of the anal fin is behind midbody (52 to 60% of SL). Pelvic fin bases are slightly behind the pectoral fin base (27 to 37% of SL), but considerably forward of the dorsal fin origin.

Ossification.—Sequence of fin ossification in *I. lockingtoni* can be derived from Table 15, which gives the meristics of cleared and stained specimens. The pectoral fins are the first to form rays at about 9.6 mm, with a complete complement of 18 to 20 rays being formed by 13.4 mm.

An 11.2-mm early flexion specimen has 4 + 4 principal caudal rays ossifying, and by

Table 12. Meristics of 25 juveniles and adults of *Icichthys lockingtoni* from over its distributional range in the eastern North Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.						
SIO 63-640	53°10'N	166°50'W	VII.2.58	108.0	23+35=58	42	30	12-17-12
SIO 63-644	52°13'N	173°33'E	? .?.58	122.0	23+35=58	43	30	12-17-12
SIO 64-673	40°04'N	124°55'W	IX.12.50	100.0	24+36=60	43	28	13-17-13
05607-60.90	36°37'N	125°47'W	VII.23.56	45.0	24+37=61	42	30	11-17-11
SIO 67-112	36°35'N	112°18'W	VI.12.67	310.0	24+36=60	42	29	13-17-12
"	"	"	"	276.0	24+34=58	42	29	12-17-12
B5104-60.100	36°17'N	126°30'W	IV.6.51	26.0	24+36=60	46	31	11-17-11
Jord. 79 (dipnet)	36°10'N	135°00'W	VI.26.73	40.0	24+34=58	43	30	12-17-11
SIO 63-405	34°57'N	129°19'W	III.29.62	98.0	23+36=59	41	29	11-17-13
"	"	"	"	193.0	23+35=58	42	30	13-17-10
SIO 64-968	33°37'N	119°52'W	III.6.54	76.0	24+34=58	42	29	12-17-11
SIO 64-364	33°13.5'N	121°27.5'W	III.8.62	42.0	23+35=58	43	30	12-17-12
"	"	"	"	43.0	24+36=60	43	32	12-17-12
H6203-80.90	33°09'N	123°13'W	III.3.62	44.0	24+35=59	42	28	12-17-13
H6204-80.90	33°09'N	123°13'W	IV.18.62	42.0	24+35=59	43	30	12-17-12
SIO 55-096	32°52'N	117°17'W	XI.11.55	234.0	23+35=58	43	29	12-17-12
SIO 58-174	32°51'N	117°17'W	III.30.56	40.0	24+36=60	43	29	12-17-12
B6208-93.30	32°44'N	117°18'W	IX.1.62	72.0	24+35=59	42	31	13-17-12
"	"	"	"	83.0	24+36=60	45	32	12-17-12
H6105-Haul 3	32°40'N	118°55'W	V.27.61	56.0	23+35=58	43	29	12-17-12
SIO 64-955	32°39'N	119°28.5'W	II.19.51	86.0	23+35=58	42	30	12-17-13
SIO 56-114	32°28'N	117°18'W	X.30.56	76.0	23+35=58	42	30	12-17-12
SIO 64-810	31°50'N	119°34'W	II.14.57	58.0	23+35=58	41	29	13-17-13
Y5206-100.29	31°42.2'N	116°43.4'W	III.9.52	33.0	23+36=59	41	29	11-17-10
P5607-97.85	30°24'N	120°51'W	VII.9.56	28.0	24+35=59	42	27	13-17-12

12.1 mm, the complete number of 9 + 8 principal rays is formed. A total count of elements (weak spines and rays) is used for the dorsal and anal fins, and these are referred to simply as rays. The dorsal and anal fins are forming on a 12.1-mm specimen and the final complement of rays for both fins is present by 13.4 mm.

Pelvic fins do not form early as in *Amarsipus* and *Psenes*, rather they form at about the same time as the dorsal and anal fins. The pelvic fins remain rather small and complete their development by 13.4 mm.

Secondary caudal rays are the last to form; a 13.4-mm specimen has 6 + 6 rays ossifying, a 20.0-mm specimen has the minimal complete count of 11 + 11 secondary rays, and a 28.6-mm specimen has the maximal complete number of 13 + 13.

The lower complete count of 58 vertebrae (23 + 35) is ossifying in a 12.5-mm specimen. Information on vertebral ossification in smaller larvae is unavailable except for a 12.1-mm larva, as vertebrae in the other specimens did not stain.

Branchiostegal rays are first ossifying on a 9.6-mm specimen which has 2 + 4 rays, and a 12.1-mm specimen has attained the final number of 3 + 4 rays. Gill rakers of the first arch are evident by 9.6 mm with the full complement of 4 + 1 + 12 gill rakers present on a 20.0-mm specimen. Haedrich (1966) reported a range in number of gill rakers of 4 to 6 + 1 + 11 to 13.

Preopercular spines do not form during the larval period of *I. lockingtoni* as they do in *Schedophilus*, *Tetragonurus*, small *Amarsipus*, and the nomeids.

Dentary teeth first appear at 12.1 mm, and premaxillary teeth at 12.5 mm; these teeth are small and increase in number with growth (Table 15).

The first evidence of scales are those ossified above the pectoral fin base in a

Table 13. Morphometrics, in mm, of larvae and/or juveniles of *Icichthys lockingtoni, Schedophilus huttoni, S. labyrinthicus,* and *S. maculatus* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
Icichthys lockingtoni									
B6310-83.60	5.2 NL	2.7	0.72	0.24	0.08	.52	-	-	-
H5202-80.90	6.8	3.4	1.2	.44	.22	.90	-	-	-
L6604-73.53	7.1	4.1	1.7	.54	.42	1.1	-	-	-
H5202-80.90	8.4	4.5	1.7	.54	.40	1.0	-	-	-
B5905-70.75	9.3	5.1	2.2	.66	.54	1.5	-	-	-
B6204-113.50	9.8	5.6	2.3	.74	.52	1.5	-	base	-
B6207-87.90	11.0	6.2	2.7	.80	.72	1.8	base	"	3.2
B6107-83.80	11.7 SL	6.4	3.1	.90	.80	2.3	"	"	3.2
J6907-73.65	12.5	6.6	3.0	.96	.76	2.2	5.6	6.9	3.4
B5905-73.80	12.7	7.0	3.4	1.3	.76	2.9	5.7	7.1	3.8
H6101-77.55	13.7	7.4	3.9	1.6	.83	3.9	5.7	7.6	4.3
H6204-60.80	14.7	7.5	4.7	1.5	1.2	4.3	6.6	7.6	4.6
H5203-90.53	15.0	7.9	4.5	1.4	1.0	4.2	6.6	8.0	4.6
B6204-80.100	19.4	10.4	6.2	2.2	1.3	6.2	8.8	10.7	6.5
B6204-70.80	21.6*	12.0	7.5	2.7	1.5	7.8	10.4	12.4	7.0
"	24.7*	14.4	8.3	2.6	2.0	8.5	11.9	14.7	9.2
B5604-107.50	31.0*	16.5	10.0	3.5	2.5	10.7	13.9	16.9	10.0
Schedophilus huttoni									
SIO 65-641	18.4 SL*	9.7	5.2	1.7	1.3	6.9	5.3	10.0	5.2
"	24.0*	12.4	7.5	2.2	1.7	10.4	6.0	12.7	8.2
"	24.8*	13.5	7.5	2.3	1.8	10.2	6.2	13.8	7.8
"	25.0*	13.7	7.8	2.4	2.0	10.5	6.7	14.0	8.3
"	33.0*	17.0	10.4	3.3	2.1	14.2	8.4	17.5	10.0
Schedophilus labyrinthicus									
Climax II	34.1*	20.8	13.0	4.2	2.8	16.2	8.8	21.2	12.0
Schedophilus maculatus									
Climax II	22.1 SL*	12.8	9.2	3.4	1.8	10.5	7.5	13.7	7.8
"	28.0*	15.8	11.0	3.8	2.2	14.2	9.8	17.5	10.0
"	77.7*	38.6	24.1	6.5	4.9	35.9	19.6	41.5	20.3

* Juvenile

20.0-mm specimen. With all 11 + 11 secondary caudal rays developed, this specimen may be classed as juvenile.

Icichthys is variable in a number of skeletal characters. Several of the characters treated below were discussed by Haedrich (1966), but not their variability.

Icichthys has a predorsal bone count of 7 to 11 (occasionally 12). The first predorsal bone precedes the first neural spine and succeeding predorsals are one per interneural space. Occasionally the posterior two or three predorsal bones are reduced to fragments and occasionally two may fuse at their distal ends. The first dorsal pterygiophore occurs as a separate entity between the 11th and 12th, 12th and 13th, or, infrequently, 13th and 14th neural spines. It usually carries two weak spines in a secondary association, but sometimes only one spine. The first anal fin pterygiophore usually carries two elements in a secondary association, but specimens with only one element or as many as three elements have been observed.

The terminal portion of the axial skeleton is somewhat variable. *Icichthys* has the primitive count of three superior hypural bones and three inferior (parhypural included as an hypural). The epural bones usually number two, but occasionally three. Perciform fishes usually have two autoge-

Table 14. Body proportions of larvae and early juveniles of four species of centrolophids, expressed as percentage of standard length (SL) and head length (HL)

Species and stage	Size range (mm)	Snout to anus/Sl	Head length/SL	Eye diameter/HL	Snout length/HL	Depth at P base/SL	Sn-D/SL	Sn-A/SL	Sn-V/SL
Centrolophidae									
Icichthys lockingtoni									
Preflexion	5.2- 8.4 NL	50-58	14-24	32-37	11-25	10-15	-	-	-
Flexion	9.3-11.0 NL	55-57	23-24	30-32	23-27	15-16	-	-	29
Postflexion	11.7-31.0 SL*	51-58	24-35	29-41	20-26	18-36	42-48	52-60	27-37
Schedophilus huttoni									
Juveniles	18.4-33.0 SL	52-55	28-32	29-33	23-26	38-43	25-29	53-63	28-34
Schedophilus labyrinthicus									
Juvenile	34.1 SL	61	38	32	22	48	35	62	35
Schedophilus maculatus									
Juveniles	22.1-77.7 SL	50-58	31-42	27-37	20	46-51	25-35	53-62	26-36

* Postflexion specimens may include both larvae and early juveniles

nous haemal spines on the vertebrae immediately preceding the ural centrum. *Icichthys* often has three autogenous haemal spines, and when only two are present there is almost invariably a doubling of the neural and/or haemal spines on one of the two vertebrae preceding the ural, usually on the second vertebra. This occurred very frequently. There are two pairs of uroneurals, one of which could be called a stegural; the other is a pair of splinter bones lying between the posterior tip of the stegural and the upper hypural bone. The stegural itself is on the posterior part of the ural centrum opposite the three superior hypurals. The neural spine of the vertebra preceding the ural is markedly reduced, as it is in most perciform fishes.

Pigmentation.—Description of pigment is based on series of reared and collected specimens. The ventral midline pigment is the dominant pigment on newly hatched larvae extending almost the length of the body from the head to the end of the notochord (Fig. 6A). Dorsal pigment consists of a series of unevenly spaced melanophores on the posterior half of the body. Lateral body pigment is lacking. Head pigment consists of small melanophores scattered around the unpigmented eyes.

Preflexion larvae maintain the earlier pigment pattern as seen in the 8.2-mm larva (Fig. 6B), except for the ventral body pigment concentrating into discrete clusters of pigment, and for heavier pigment forming over the head. There is a suggestion of an eye bar forming, but it is not conspicuous like those found in *Amarsipus*, *Tetragonurus atlanticus*, and *T. cuvieri*.

By late flexion (ca. 10.4 mm) (Fig. 6C), the dorsal margin pigment extends forward almost to the head. Dashes of lateral line pigment extend along the posterior half of the body. Between the lateral line and dorsal margin a line of dorsal-lateral spots extends for most of the body length. There is considerable pigment in the region of the developing caudal fin including over the hypurals, between principal caudal rays and on the adjacent fin fold. Head pigment has intensified; pigment is present on the tips of both jaws.

The 13.5-mm postflexion specimen (Fig. 6D) is similar to the preceding specimen, but with intensification of pigment on the head, the tail portion of the body, and over the abdomen. The weak eye bar is still present.

By 20.0 mm (Fig. 6E) pigment has spread over the entire body. Pigment is heavy on the lower part of the head. The original dorsal margin pigment is concentrated into a few conspicuous spots along the posterior

Table 15. Meristics of cleared and stained larvae and juveniles of *Icichthys lockingtoni* (specimen between dashed lines is undergoing notochord flexion)

Station	Size (mm)	Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
										Prem.	Dent.
L6604-73.53	7.1 NL	-	-	LP	-	-	-	-	-	-	-
"	9.6	-	-	2-R 0-L	-	-	-	2+4	0+1+5	-	-
S5805-77.50	11.2	-	-	3	-	0-4+4-0	-	2+4	0+1+5	-	-
H6107-80.60	12.1 SL	25	25	12	I,3	0-9+8-0	24+30=54†	3+4	1+1+9	0	3
B6207-93.90	12.5	37	27	13	I,4	0-9+8-0	23+35=58	3+4	3+1+9	2	6
B6207-87.65	13.4	42	29	19	I,5	6-9+8-6	24+36=60	3+4	3+1+10	10	7
S5604-83.60	16.7	44	31	18	I,5	4-9+8-4	24+37=61	3+4	3+1+10	11	14
B6204-70.80	20.0*	43	28	20	I,5	11-9+8-11	24+35=59	3+4	4+1+12	20	13
"	28.6*	43	30	19	I,5	13-9+8-13	24+35=59	3+4	5+1+11	22	23

* Juvenile

† Vertebrae not completely developed

half of the tail and similarly the ventral pigment is concentrated into a few spots. All fins are pigmented.

Genus *Schedophilus*

Juveniles of three of the eight species of *Schedophilus* were sampled from the eastern South Pacific, all dipnetted under jellyfish. As mentioned in earlier sections, we have had the opportunity to study radiographs of eight species of *Schedophilus*, and wish again to emphasize the taxonomic value of the arrangements of predorsal bones and pterygiophores in relation to vertebral spines.

Schedophilus huttoni

(Waite, 1910)

Figure 8

Literature.—This species has only rarely been reported in the literature. Haedrich and Nielsen (1966) reported a ca. 40-mm specimen from the stomach of *Alepisaurus* taken in the Pacific at 34°24′S, 94°45′W. Craddock and Mead (1970) listed two specimens, 21 and 59 mm, from cruise 13 of the R/V ANTON BRUUN off Chile (32°59′–33°05′S, 74°57–59′W; 33°20′S, 73°41–42′W). Recently, Trunov (1969) reported on 24 specimens ranging in size from 420 to 720 mm from the South Atlantic. Smith (1966) described a very similar form, *Coroplopus dicologlossops*, from South Africa.

Material.—Five early juveniles, 18.4 to 33.0 mm, dipnetted off Juan Fernandez Islands, were available to us from the SIO collection.

Distribution.—Known from Australia, New Zealand, the eastern South Pacific off Chile, and the South Atlantic, this species was recorded as far north in the Atlantic as 18°S by Trunov (1969). This distribution indicates a circumglobal distribution in the southern oceans.

Distinguishing Characters.—*Schedophilus huttoni* is unique in its high number of dorsal elements (60 to 63 in our specimens —see Table 16). It is the highest total dorsal count among the stromateoid fishes, and ranges from 56 to 63 (Trunov, 1969). The vertebral counts of 12 + 19 to 20 = 31 or 32 and the total anal fin ray counts of 33 to 38 are unique among the centrolophids. The early juveniles possess strong preopercular spines as do those of *S. labyrinthicus* and *S. maculatus*. These preopercular spines are better developed in this genus than any other treated in this paper.

Meristics.—Vertebrae 12 + 19 to 20 = 31 or 32 (average 31.6); dorsal 60 to 63 (average 61.4); anal 33 to 38 (average 36.8); principal caudal rays 9 + 8; secondary caudal rays 10 to 12 dorsal + 9 to 11 ventral (average 10.7 + 9.7) (Table 16).

Morphometrics.—Morphometrics for the available specimens are presented in Table 13 and body proportions are compared with other centrolophids in Table 14. *S. huttoni*

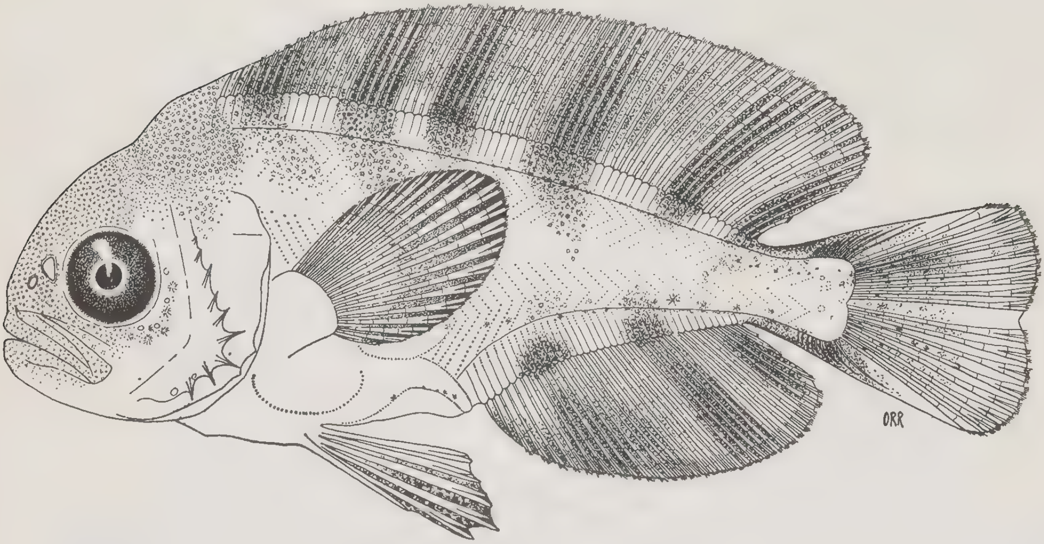

Figure 8. Early juvenile of *Schedophilus huttoni* (Centrolophidae), 25.0 mm.

is markedly more slender-bodied and has its dorsal fin originating farther forward on the body than in *S. labyrinthicus* or *S. maculatus.*

Ossification.—Data on the sequence of ossification are lacking inasmuch as only five early-juvenile specimens are available. Radiographs were made of these, and one specimen was cleared and stained. The sequential arrangement of anal fin pterygiophores in relation to haemal spines, based on the cleared and stained specimen, is given in Table 4.

Pigmentation.—Pigment on the early juvenile of *S. huttoni* is sparse compared to *S. maculatus* and *S. labyrinthicus* (compare Fig. 8 with Figs. 9 and 10). The head is heavily pigmented on the jaws, the snout, and over the eye, while the preopercle

Table 16. Meristics of juveniles and an adult of three species of *Schedophilus* from the eastern South Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
S. huttoni									
SIO 65-641(dipnet)	33°31'S	78°49.7'W	XII.12.65	18.4	12+19=31		61*	37*	7-17-6
"	"	"	"	24.0	12+20=32		60*	38*	9-17-8
"	"		"	24.8	12+19=31		60*	33*	10-17-9
'	"	"	'	25.0	12+20=32		63*	38*	10-17-9
"	"	"	"	33.0	12+20=32		63*	38*	12-17-11
S. labyrinthicus									
Climax II(dipnet)	24°42'S	155°03.5'W	X.3.69	34.1	10+15=25	VII	26	III,18	11-17-10
SIO 65-650	33°34.3-35.5'S	78°54.9-55.5'W	XII.14.65	560.0	10+15=25	VIII	27	III,19	11-17-10
S. maculatus									
Climax II(dipnet)	24°42'S	155°03.5'W	X.3.69	22.1	11+18=29	IX	28	III,23	11-17-10
'		'	"	28.0	11+18-29	VIII	28	III,23	10-17-10
Climax II(dipnet)	24°34'S	154°50'W	X.9.69	77.7	11+18=29	IX	27	III,23	11-17-10

* Dorsal and anal counts are given for total number of elements, including weak spines

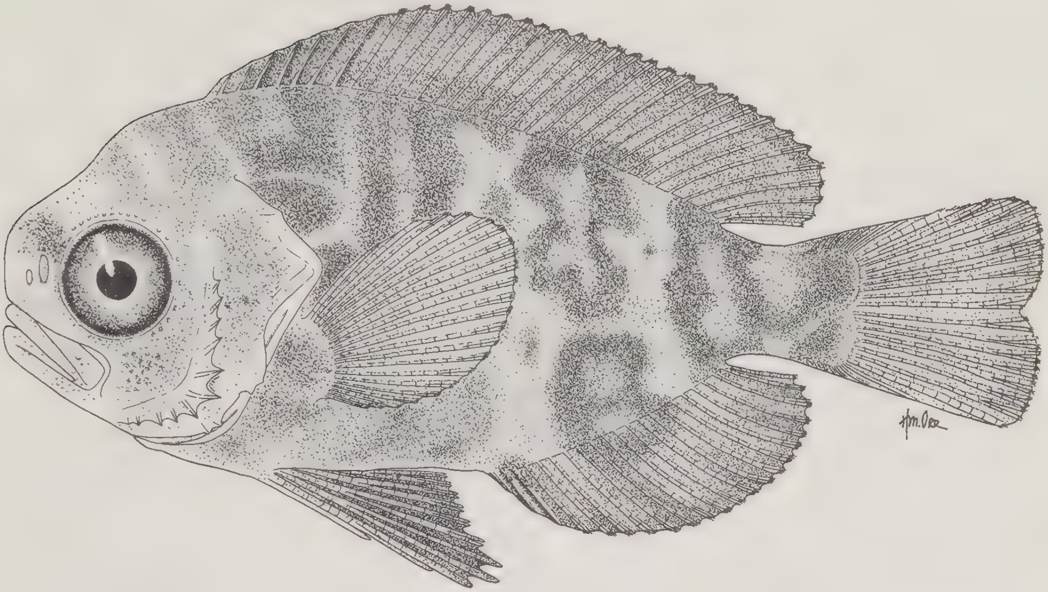

Figure 9. Early juvenile of *Schedophilus labyrinthicus* (Centrolophidae), 34.1 mm.

and opercle are almost unpigmented. Pigment on the body is concentrated along the body margin in patches which are extensions of pigment bands on the dorsal and anal fin membranes. The pectoral and pelvic fins are rather heavily pigmented, while the caudal fin is pigmented only near its base.

Schedophilus labyrinthicus
McAllister and Randall, 1975
Figure 9

Literature.—There is a problem as to what scientific name to apply to this species. It obviously is closely related to *S. ovalis*, and may prove to be a geographical variant of that species. Stehmann and Lenz (1973) placed three nominal species from the southern oceans, i.e., *Seriolella velaini* Sauvage, 1879, *Seriolella christopherseni* Sivertsen, 1946, and *Seriolella* spec. nov. (McAllister and Randall, MS) in the synonymy of *Schedophilus ovalis*. McAllister and Randall (1975) disagreed and described their specimens as *Schedophilus labyrinthicus*, noting lower dorsal and anal fin ray counts, differences in body proportions, and disjunct distributions as the justification for separating their species from *S. ovalis*. Even if the specimens from the southern oceans are distinct from *S. ovalis*, another problem needs to be resolved—viz. whether the three described species are distinct from one another. Both *S. labyrinthicus* and *S. christopherseni* possess two predorsal bones similarly arranged, a character shared in common with *S. ovalis*. This character could not be checked in *S. velaini* as the type specimen is presumably lost. *S. velaini* was collected from off St. Paul Island in the Indian Ocean, *S. christopherseni* from Tristan da Cunha in the South Atlantic. *S. labyrinthicus* is known from several localities in the South Pacific between Chile and Australia. Eventually it may be determined that all southern ocean forms belong to a single species, in which case both *S. velaini* and *S. christopherseni* would have priority over *S. labyrinthicus*. Fortunately, we do not have to make the decision whether *S. velaini* is well enough described to be definitely assigned to the southern "ovalis-like" species, or whether instead *S. christopherseni* should be used. We hope that our illustration of the southern form may stimulate a comparison with similar-sized specimens of *S. ovalis*.

Material.—A 34.1-mm juvenile dipnetted under a medusa in the south central gyre and a 560-mm adult (SIO 65-650) from Juan Fernandez Island were examined. In addition, radiographs of two specimens, one from an unknown locality and the other from off Lord Howe Island, Australia, were examined through the courtesy of Dr. R. L. Haedrich.

Distribution.—This species is now known from Juan Fernandez off Chile, Easter, and

Rapa Iti Islands, from Lord Howe Island off Australia and from the central water mass of the South Pacific. The planktonic juvenile is obviously the connecting link between widely separate populations.

Distinguishing Characters.—*Schedophilus labyrinthicus* is distinguished by osteological characters, meristics, pigmentation and morphometrics. There are only two predorsal bones and less than 20 anal fin rays. The blotched pigment pattern is different from the banded pattern of *S. maculatus* and *S. huttoni* at this stage, but a 78-mm juvenile of *S. maculatus* also has heavily mottled pigment. The body is less deep than the 44-mm specimen of *S. ovalis* illustrated by Padoa (1956). Unfortunately Padoa's specimen was bleached. The difference in body depth, also found in adults, supports the distinctness of *S. labyrinthicus* from *S. ovalis*. Whether or not *S. labyrinthicus* is distinct from *S. velaini* and *S. christopherseni* cannot be determined from our material.

Meristics.—Vertebrae 10 + 15 = 25; first dorsal VII to VIII; second dorsal 26 to 27; anal III, 18 to 19; principal caudal rays 9 + 8; secondary caudal rays 11 dorsal + 10 ventral (Table 16).

Morphometrics.—Morphometrics for the two available specimens are given in Table 13 and body proportions are presented in Table 14.

Ossification.—No ossification data are available. The sequential arrangement of anal fin pterygiophores in relation to haemal spines, based on radiographs, is given in Table 4.

Pigmentation.—Juveniles of this species are heavily pigmented over the head, body, and fins (Fig. 9). The pigment on the head is broken into areas of darker and lighter pigment, with darker patches on the snout, over the eye, and on the opercle and preopercle. The body has irregular patches of pigment that resemble the vertical barring of other species. The patches are irregular in outline with lighter areas in the center. Pigment is heavy on the pelvic, pectoral, and caudal fins. The dorsal and anal fins are mottled like the pigment on the body.

Schedophilus maculatus
Günther, 1860
Figure 10

Literature.—This species has not been previously recorded for the eastern Pacific. The type specimen described by Günther (1860), 37 mm SL, was from the "Sea of China." *Schedophilus marmoratus* Kner and Steindachner, 1866, and *Hoplocoryphis physaliarum* Whitley, 1933, from Australia are probably synonyms (Haedrich, 1967).

Material.—Three juveniles were dipnetted under jellyfish; two of these were taken with *S. labyrinthicus*, the other separately. Radiographs of Australian material including the lectotype of *Hoplocoryphis physaliarium* were examined.

Distribution.—Our specimens were taken in the central water mass of the South Pacific. This species may prove to have a circumglobal distribution in the southern oceans.

Distinguishing Characters.—The vertebral count of 11 + 18 = 29 for *S. maculatus* is unique among centrolophids. The dorsal fin counts of VIII to IX, 27 to 28, and anal fin counts of III, 23 for this species also are unique in the genus *Schedophilus*.

Meristics.—Vertebrae 11 + 18 = 29; first dorsal VIII to IX; second dorsal 27 to 28; anal III, 23; principal caudal rays 9 + 8; secondary caudal rays 10 to 11 dorsal + 10 ventral (Table 16).

Morphometrics.—Morphometrics for the available specimens are presented in Table 13 and body proportions in Table 14. The body of *S. maculatus* is relatively deep (46 to 51% of SL) and the eyes are large (27 to 37% of HL).

Ossification.—Ossification data based on cleared and stained specimens are not available. The sequential arrangement of anal fin pterygiophores in relation to haemal spines as read from radiographs is presented in Table 4.

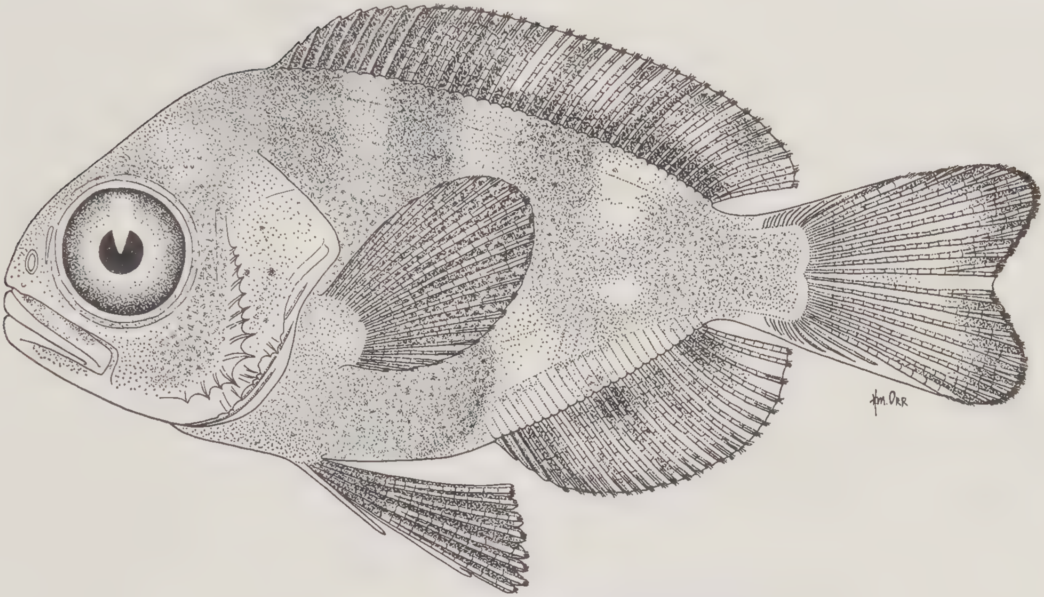

Figure 10. Early juvenile of *Schedophilus maculatus* (Centrolophidae), 22.1 mm.

Pigmentation.—Pigment on the 22.1-mm specimen is heavily developed on the head and body (Fig. 10). The head is more heavily pigmented over the eye, on the snout, and on the preopercle than on the lower jaw and the opercle. Pigment is present over the entire body but chiefly in four vertical bands; the first band at the dorsal fin origin and the last at the termination of the dorsal. The pectoral and pelvic fins are heavily pigmented as is the anterior portion of the dorsal fin. Pigment on the remainder of the dorsal fin and the anal fin is patchy. Pigment on the caudal fin is heaviest along its outer margin.

Family TETRAGONURIDAE

The tetragonurids are among the more specialized stromateoid fishes. The body is slender and elongate with a long caudal peduncle (especially so in *T. cuvieri*) supporting lateral keels on each side near its end. Scales on the body and head are keeled and strongly adherent. The two dorsal fins are not separated. Spines in the first dorsal fin are much shorter than rays in the second dorsal. Dorsal spines number (X) XI to XVIII (XXI)[3] and dorsal rays 10 to 13 (17). The anal fin origin is slightly behind that of the second dorsal. The anal fin has I, rarely II spines and 9 to 12 (16) rays. The caudal fin has 17 principal rays (15 branched), 9 to 13 dorsal secondary rays, and 9 to 12 ventral secondary rays. The pelvic fins are short, with a complement of I, 5. The pectoral fins are rather small with 14 to 18 (21) rays.

Juveniles and adults of this family have 39 to 54 (58) vertebrae, 6 (occasionally 5) branchiostegal rays, 2 + 2 hypurals including the parhypural, 2 epurals, and no predorsal bones. The dorsal fin origin follows the neural spine of vertebrae 5 to 8. The first dorsal fin pterygiophore and first anal pterygiophore each support a single spine in a secondary association.

Genus *Tetragonurus*

The family is comprised of one genus with three species, all of which occur in the eastern Pacific. Juveniles and adults of the three species are most readily separated by meristic characters, whereas larvae are most simply separated by differences in pigmentation.

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[3] Values in parentheses extending ranges are from the literature; the basic counts are from specimens examined by us.

Comparative Morphometrics

The morphometrics of the three species of *Tetragonurus* are not strikingly different during larval development (Table 10). Morphometrics for only three postflexion species are available for *T. pacificus*, but fairly complete size series are available for *T. cuvieri* and *T. atlanticus*.

Head Length.—On the smallest specimens of *T. cuvieri* and *T. atlanticus* the head is smaller than on larger preflexion specimens. On a newly hatched specimen of *T. cuvieri* the head is only 11% of NL, but on a 6.6-mm specimen it has increased to 23%. On the smallest specimen of *T. atlanticus*, 3.3 mm NL, the head is only 14% of NL. The head increases rapidly in size relative to other body parts, for by 4.2 mm it is 26% of NL. Head length is 24 to 27% of NL during flexion of *T. cuvieri*, and 25 to 32% of SL in postflexion specimens. The head may be slightly larger on flexion and postflexion specimens of *T. atlanticus*, ranging 27 to 30% of NL during flexion and 30 to 35% of SL on postflexion specimens. On postflexion specimens of *T. pacificus*, HL is 30 to 33% of SL.

Eye Diameter.—The eye is round on postflexion specimens of the three species, but is off round to bluntly dumbbell-shaped on preflexion larvae. Except for the two early preflexion larvae with small heads (discussed above), eye diameter is about 30% of HL throughout larval development, ranging from 27 to 34% of HL in *T. cuvieri*, 28 to 34% of HL in *T. atlanticus* and 29 to 33% of HL in *T. pacificus*.

Snout Length.—The snout is somewhat more pointed in tetragonurids than in the nomeids, but is still moderate. The snout increases in length relative to head length in preflexion larvae of *T. cuvieri* from 20 to 22% of HL to about 28%, and then stabilizes; in later stages it ranges between 23 to 31% of HL. The snout shows little difference in relative length among larvae of *T. atlanticus* between 4.2 to 17.2 mm: 24 to 29% of HL, with all but one value between 27 to 29%. On larvae of *T. pacificus*, snout length is 27 to 32% of HL.

Snout to Anus.—As is evident from Table 10, there is little if any change in the proportionate distance from snout to anus during larval development. In *T. cuvieri* the snout-anus length averages 60% of SL, with a range of 56 to 67%. In *T. atlanticus*, the snout-anus length averages 67% of SL, with a range of 63 to 71%. This is the most marked difference in body proportions noted for these two species. In *T. pacificus* the proportionate values are intermediate, 62 to 65% of SL.

Body Depth.—Small preflexion larvae of *T. cuvieri* and *T. atlanticus* are considerably more slender than larvae undergoing flexion or in postflexion. In *T. cuvieri* the increase in relative body depth is from 10 to 18% of NL immediately prior to flexion, remaining at 18 to 20% during flexion, and increasing only slightly thereafter, 20 to 22 (25)% of SL. In *T. atlanticus* the increase in relative body depth occurs more rapidly during the preflexion stage, from 13% to about 20% of NL; it averages 20% during flexion and about 26% of SL during postflexion (range 24 to 28%). In body depth, *T. pacificus* averages 27% of SL. Apparently, larvae of *T. cuvieri* are somewhat more slender than those of the other two species.

Snout to Fin Origins.—Measurements to the origin of fins (dorsal, anal, and pelvic) can be made on later-stage larvae only after fins are developed. Measurement of the snout to the origin of the spinous dorsal can be made only on postflexion larvae, but meaningful measurements on snout-anal fin origin or snout-pelvic fin base can be made on some flexion larvae as well as all postflexion larvae. Only slight differences in these proportionate measurements exist among the three species (Table 10). In relation to the longer gut length noted for *T. atlanticus*, the origin of the anal fin is also somewhat farther back on the body, 68% of SL, as compared to 63% of SL in *T. cuvieri* and 65% in *T. pacificus*.

Tetragonurus atlanticus
Lowe, 1839
Figure 11

Literature.—Grey (1955) reported two specimens of *Tetragonurus atlanticus* from the eastern Pacific, a 20-mm SL specimen from Dana Station 3558 at 00°18′S, 99°07′W (September 18, 1928) and a 12.0-specimen from CalCOFI Station 5009-90.175 occupied at 28°34.5′N, 127°38′W (September 15, 1950). She illustrated a series of flexion and postflexion larvae. Abe (1955a) reported an adult taken off Japan.

Material.—Thirty-four collections of larvae from the eastern tropical Pacific and five collections from the central North Pacific were examined. Nine trawl collections from the eastern tropical Pacific contained the 16 juveniles listed in Table 17.

Distribution.—*T. atlanticus* is widely distributed in the tropical and subtropical eastern Pacific. In the EASTROPAC area it was found from 5°N to 20°S, west of the Galapagos Islands (Fig. 12). In the central Pacific, specimens were taken off Hawaii to 33°N in the central water mass (Fig. 5).

Distinguishing Characters.—JUVENILES. *T. atlanticus* is distinguished from the other two species by the number of vertebrae and the number of dorsal spines (Table 1).

LARVAE. Preflexion and postflexion larvae are characterized by the number of myomeres (44 to 46) and by their pigmentation. Pigment is lacking on the tip of the tail but present over the rest of the body. Similar stages of *T. cuvieri* are as heavily pigmented over the body, but in addition have pigment on the tip of the tail. During most of the larval period, *T. pacificus* larvae develop pigment only over the anterior portion of the body.

Meristics.—Vertebrae 23 or 24 + 20 to 22 = 44 to 46 (average 44.7); first dorsal XIV or XV (average 14.3); second dorsal 10 to 12 (average 11.3); anal I, 9 to 11 (average I, 10.2); principal caudal rays 9 + 8; secondary caudal rays 9 or 10 dorsal + 9 or 10 ventral (average 9.2 + 9.3).

Meristics of 16 specimens from about 4°S to the equator and from about 96°W to about 121°W are given in Table 17. No geographical variation of any count is indicated.

Morphometrics.—Morphometrics of a size series are presented in Table 18, and body proportions in Table 10. A discussion of the morphometrics of the three species of *Tetragonurus* is presented in an earlier section.

Ossification.—Meristics of seven cleared and stained specimens are presented in Table 19. The principal caudal rays are the earliest to develop with 8 + 7 rays formed at 7.2 mm. The complete number of 9 + 8 principal caudal rays is formed by 8.6 mm (Fig. 11D). The bases of the second dorsal and anal fins appear at 7.2 mm, and by 8.6 mm, each of these fins has developed its full complement of rays.

Rays appear in the pectoral fin at about the same size as in the second dorsal and anal fins, and the pectoral fin is complete by 13.2 mm.

At 10.5 mm, the first dorsal fin has developed its full set of 15 spines, and the pelvic fin and secondary caudal rays are partially formed. The pelvic fin is complete by 13.2 mm, and all secondary caudal rays are developed by 19.7 mm.

The fins of *T. atlanticus* differentiate earlier than in *T. cuvieri*, but not as rapidly as in *T. pacificus*. This generalization applies as well to the size at notochord flexion and the ossification of vertebrae and other structures.

Thirty-one vertebrae are ossified by 8.0 mm, and all 45 (24 + 21) vertebrae are formed by 10.5 mm. A full set of 2 + 4 branchiostegal rays are ossified by 7.2 mm.

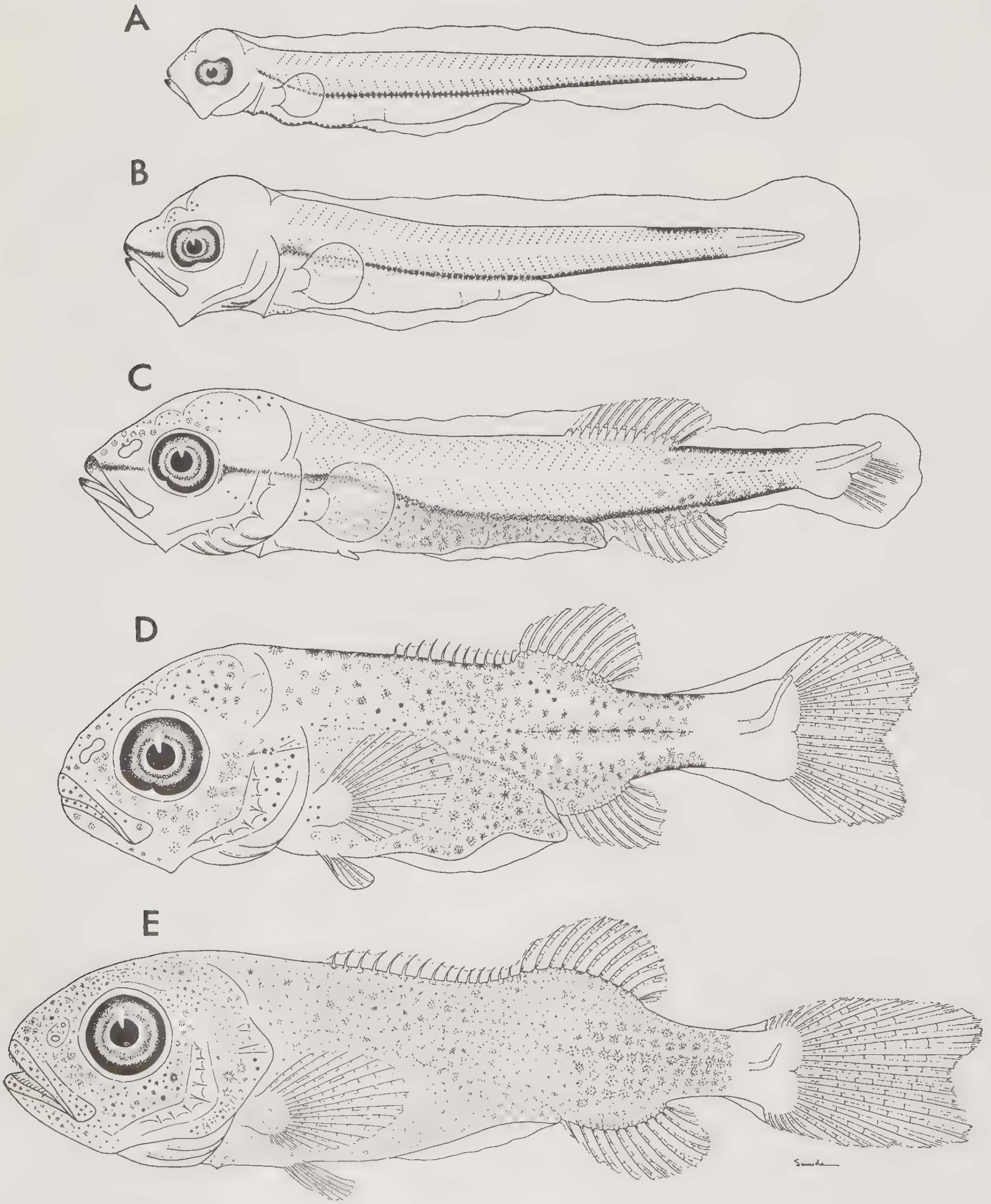


Figure 11. Developmental stages of *Tetragonurus atlanticus* (Tetragonuridae). A—3.0-mm preflexion larva; B—4.6-mm preflexion larva; C—7.6-mm early flexion larva; D—8.5-mm postflexion larva; E—17.2-mm postflexion larva.

Table 17. Meristics of 16 juveniles of *Tetragonurus atlanticus* from the eastern tropical Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Jord. 65.164	00°30'S	96°42'W	IX.12.71	53.9	23+21=44	XIV	11	I,10	9-17-9
Jord. 65.214	00°30'S	97°13'W	IX.28.71	55.0	24+21=45	XIV	12	I,10	9-17-9
Jord. 65.160	01°29.5'S	96°42.1'W	IX.11.71	52.1	23+22=45	XV	11	11	9-17-9
T.C. 51.059	03°00'S	119°40'W	XI.10.70	21.8	24+20=44	XIV	11	I.10	10-17-10
T.C. 51.070	03°02'S	121°00'W	XI.13.70	24.0	23+21=44	XIV	12	I,11	9-17-10
"	"	"	"	25.8	23+22=45	XV	10	I,11	9-17-9
T.C. 51.066	03°10'S	120°19.5'W	XI.12.70	20.8	24+21=45	XIV	11	I,10	9-17-9
"	"	"	"	32.2	24+22=46	XIV	12	I,10	9-17-9
T.C. 51.071	03°12'S	121°27'W	XI.14.70	25.1	24+21=45	XV	12	I,11	10-17-10
"	"	"	"	55.7	23+21=44	XIV	I,11	I.11	9-17-10
T.C. 51.063	03°44'S	119°30'W	XI.12.70	18.8	23+21=44	XIV	11	10	9-17-9
"	"	"	"	19.2	24+21=45	XV	11	I,10	10-17-10
"	"	"	"	41.0	23+21=44	XV	10	I,9	9-17-9
"	"	"	"	42.0	24+21=45	XIV	11	I,9	9-17-9
T.C. 51.048	04°02'S	118°48'W	XI.8.70	13.2	24+21=45	XIV	12	I,10	9-17-9
"	"	"	"	19.7	23+21=44	XIV	12	11	9-17-9

Gill rakers of the first arch appear on the lower arch at 8.0 mm, and by 19.7 mm, 4 + 1 + 8 are formed.

A fringe of three small spines develops along the outer margin of the preopercle at about 7.2 mm and increases to eight spines at 17.2 mm. These spines are more conspicuous in *Tetragonurus* than in the nomeids. They are later resorbed in the opercular tissue.

Premaxillary and dentary teeth first appear at 7.2 mm and increase in number with

Table 18. Morphometrics, in mm, of larvae of *Tetragonurus atlanticus* and of larvae and a juvenile of *T. pacificus* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
Tetragonurus atlanticus									
ETP 20.222	3.0 NL	1.9	0.42	0.20	0.10	0.40	-	-	-
ETP 20.191	4.2	2.9	1.1	0.36	0.32	0.84	-	-	-
ETP 20.224	4.6	3.1	1.2	0.36	0.30	0.86	-	-	-
ETP 46.071	4.9	3.3	1.1	0.38	0.30	0.78	-	-	-
ETP 45.131	5.8	3.7	1.5	0.42	0.40	0.96	-	-	-
ETP 20.064	7.3	4.9	2.0	0.62	0.44	1.5	-	-	2.5
ETP 13.105	7.6	4.9	2.2	0.66	0.62	1.5	-	-	2.5
ETP 46.059	7.6	5.2	2.2	0.62	0.62	1.4	-	-	2.6
ETP 13.117	7.8	5.4	2.2	0.68	0.60	1.8	-	-	2.7
ETP 50.077	8.1	5.4	2.4	0.72	0.70	1.8	-	5.5	2.9
ETP 45.090	8.5 SL	5.9	3.0	1.0	0.80	2.4	4.1	6.0	2.8
J7210-31.139	10.5	6.7	3.2	1.1	0.88	2.5	4.2	6.9	3.8
"	12.4	7.9	4.1	1.2	1.2	3.2	4.9	8.1	4.2
ETP 20.193	17.2	12.2	5.6	1.7	1.6	4.4	7.2	12.4	6.4
Tetragonurus pacificus									
ETP 30.055	8.9 SL	5.5	2.7	0.80	0.80	2.6	3.8	5.6	3.0
"	9.4	6.1	2.8	0.80	0.90	2.5	3.8	6.2	2.8
Hawaii 70-9-2	19.5 *	12.4	6.4	2.1	1.7	5.2	7.8	12.6	6.8

* Juvenile

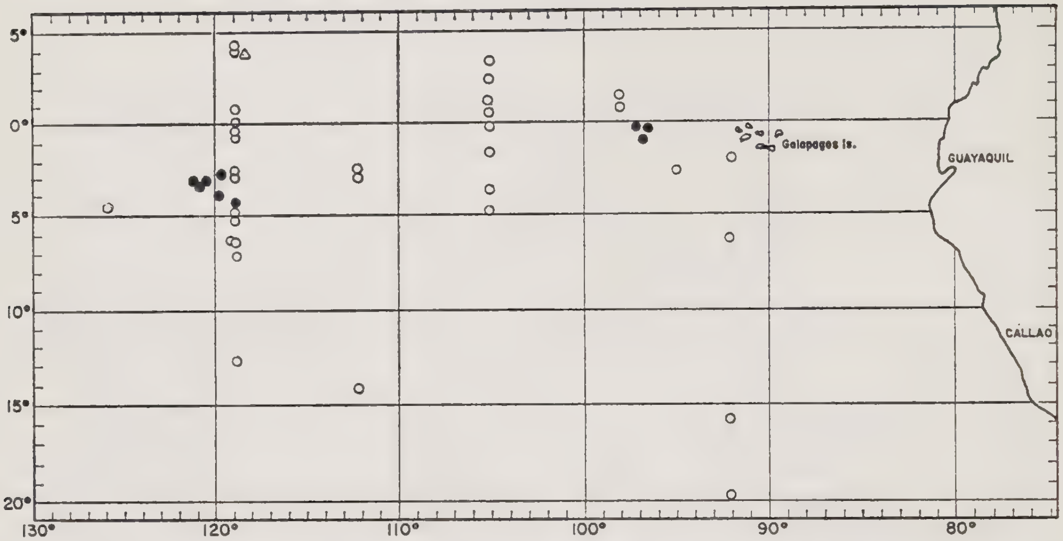


Figure 12. Occurrences of *Tetragonurus atlanticus* larvae (open circles) and juveniles (closed circles) and of a *T. pacificus* larva (open triangle) in the eastern tropical Pacific.

size. The dentary teeth are longer, broader, and more blade-like compared to the small, pointed teeth on the premaxillary. A general discussion of dentition in *Tetragonurus* and other stromateoids is given in an earlier section.

Scales are evident on a 17.2-mm specimen (Fig. 11E) and were seen on a cleared and stained specimen of 19.7 mm. The 17.2-mm specimen has only 6 + 6 secondary caudal rays, but the 19.7-mm specimen has a full complement of 9 + 9, thereby classifying it as an early juvenile.

Pigmentation.—Preflexion larvae have conspicuous pigment on the ventral margin of the body. Pigment is lacking, however, on the tip of the notochord. Postflexion larvae add pigment over the head and body except the base of the caudal fin which remains unpigmented.

Yolk-sac larvae have a continuous line of ventral pigment on either side of the body extending from the head to the tip of the notochord; forward of the anus this line of pigment is over the gut. Dorsal pigment is limited to a single median line on the last 8 to 12 myomeres extending to the tip of the notochord. There is pigment on the head around the developing mouth and scattered pigment below the yolk-sac and gut.

Simultaneous with the onset of pigmentation of the eyes, pigment is lost at and near the tip of the notochord (Fig. 11A). In contrast, pigment remains at the tip of the tail in *T. cuvieri* while it is absent in *T. atlanticus* until at least 17.2 mm.

Preflexion larvae add little pigment to what is found in the yolk-sac stage. By 4.6 mm (Fig. 11B), a line of pigment has formed on the snout from the tip of the upper jaw to the anterior margin of the eye, and scattered melanophores are present over the brain. Dorsal pigment which begins just anterior to the terminal one or two myomeres, extends forward about 10 myomeres; viewed from above, this is seen to be a double line.

Flexion larvae add pigment over the head, over the gut, and on the caudal peduncle (Fig. 11C). Pigment develops in a line posterior to the eye, forming a prominent eye bar from the snout to the edge of the opercle which connects posteriorward with

Table 19. Meristics of cleared and stained larvae and a juvenile of *Tetragonurus atlanticus* (specimens between dashed lines are undergoing notochord flexion)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 20.191	4.2 NL	-	-	-	LP	-	-	-	-	-	-	-
ETP 46.071	5.0	-	-	-	LP	-	-	-	-	-	-	-
ETP 20.064	7.2	-	base	base	LP	-	0-8+7-0	none stained	2+4	-	2	1
ETP 50.077	8.0	-	10	10	11	-	0-8+7-0	21+10=31[†]	2+4	0+0+8	6	3
J7210-31.139	10.5 SL	XV	11	I,10	16	I,3	3-9+8-3	24+21=45	2+4	1+1+8	7	10
T.C. 51.048	13.2	XIV	12	I,10	17	I,5	8-9+8-8	24+21=45	2+4	3+1+8	10	16
"	19.7[*]	XIV	12	I,10	17	I,5	9-9+8-9	24+21=45	2+4	4+1+8	14	22

[*] Juvenile

[†] Vertebrae not completely developed

the line of pigment above the gut. Pigment forms along the lateral line and on the margins of the body on the caudal peduncle.

Postflexion larvae add pigment over the body except adjacent to the caudal fin. By 8.5 mm (Fig. 11D), pigment is heavy at the lateral line on the trunk, on the dorsal and ventral margin of the anterior half of the caudal peduncle and on the dorsal margin anterior to the second dorsal fin. The eye bar is still present behind the eye. By 17.2 mm (Fig. 11E), the head and body are uniformly pigmented except for the base of the caudal fin which remains unpigmented.

Tetragonurus cuvieri
Risso, 1810
Figure 13

Literature.—Although at one time considered a rare fish (Thompson, 1919; Fitch, 1949, 1951), *T. cuvieri* is now known to be rather common offshore (Tanonaka, 1957; Larkins, 1964). Fowler (1928), Welander and Alverson (1954), Grey (1955), Neave (1959), and Berry and Perkins (1966) gave additional records for the eastern and central North Pacific, and Craddock and Mead (1970) gave records from the South Pacific off Chile and Abe (1955) from off Japan. Sparta (1929) described and illustrated two late stage larvae and Grey (1955) illustrates a series of larvae.

Material.—Collections of larvae obtained on the NORPAC expedition and CalCOFI cruises from the North Pacific were examined, together with eight juveniles.

Distribution.—*T. cuvieri* is broadly distributed in the transition waters of the California Current and offshore in the central water mass as is shown for its distribution on NORPAC (Fig. 5). It is a temperate water form which replaces *T. atlanticus* north of about 34°N in the central Pacific and north of about 22°N in the eastern Pacific.

Distinguishing Characters.—JUVENILES. *T. cuvieri* is distinguished by its high number of vertebrae and dorsal fin spines (Table 1).

LARVAE. Preflexion and postflexion larvae are characterized by the number of myomeres (51 to 54) and by their pigmentation. Pigment is present at the tip of the notochord and at the base of the caudal fin (Fig. 13). Similar pigment is lacking in the other species of *Tetragonurus*.

Meristics.—Vertebrae 26 or 27 + 25 to 28 = 51 to 54 (average 52.1); first dorsal XV to XVIII (average 17.1); second dorsal 11 to 13 (average 12.1); anal I to II, 10 to 12 (average I, 11.3); principal caudal rays 9 + 8; secondary caudal rays 9 to 13 dorsal + 9 to 12 ventral (average 10.5 + 10.3).

Meristics of seven specimens from about 26°N to about 34°N and about 115°W to about 132°W are given in Table 20. No geographical variation of any count is indicated.

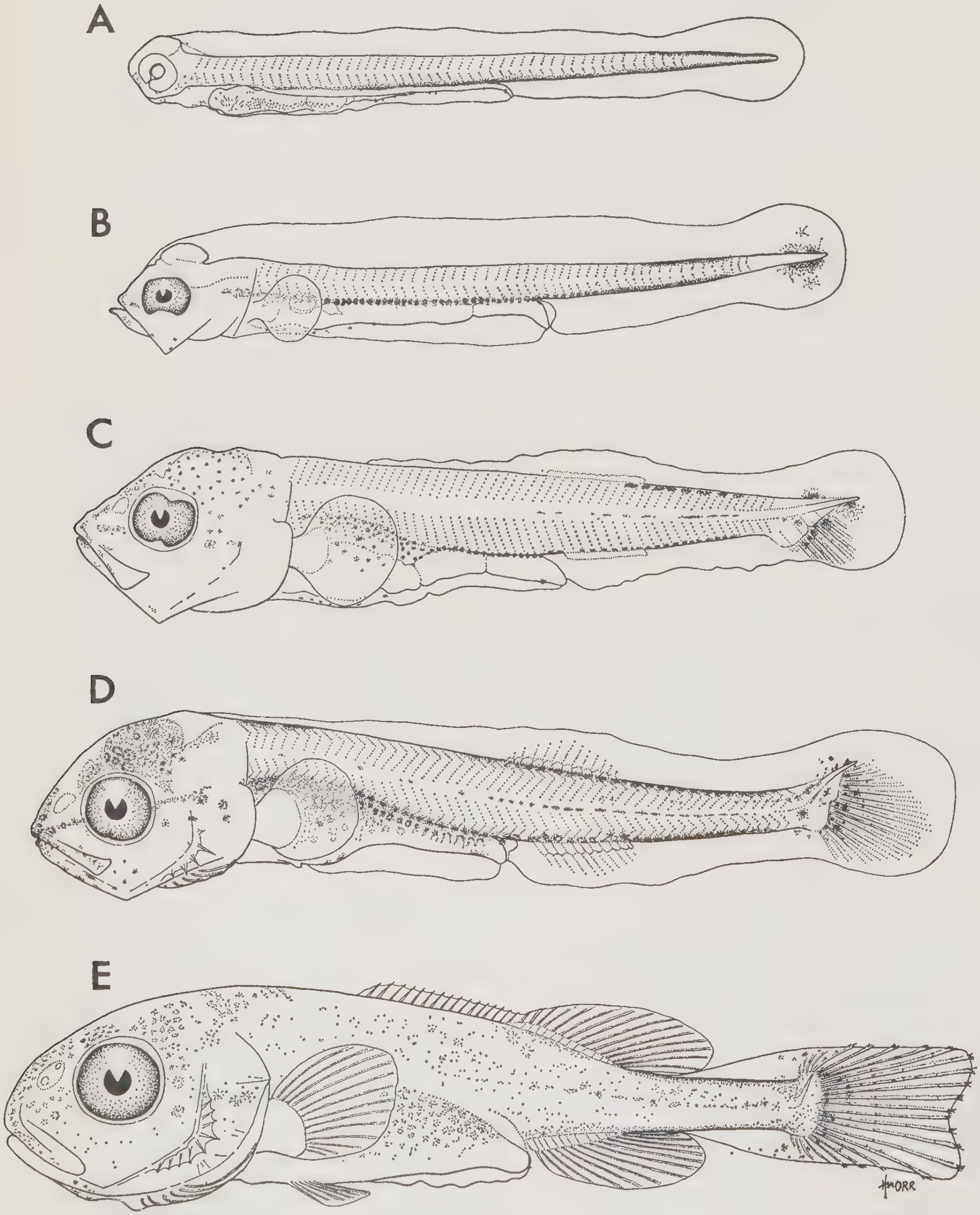


Figure 13. Developmental stages of *Tetragonurus cuvieri* (Tetragonuridae). A—4.1-mm preflexion larva; B—4.9-mm preflexion larva; C—7.6-mm early flexion larva; D—10.1-mm late flexion larva; E—17.0-mm postflexion larva.

Table 20. Meristics of seven juveniles of *Tetragonurus cuvieri* from the eastern Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
SIO 62-754	34°00'N	132° W	I.18.54	40.0	26+25=51	XVII	12	I,11	-
"	"	"	"	41.0	27+25=52	XVII	12	-	-
SIO 50-298	33°20'N	118°17.3'W	XII.8.50	54.0	27+26=53	XVIII	12	I,12	10-17-10
SIO 63-500	80 miles	off S.Diego	VIII.?.63	26.8	27+26=53	XVIII	12	I,12	9-17-9
SIO 66-006	32°31.5 - 31.6'N	117°39.4- 30.4'W	III.13.66	47.0	27+26=53	XVI	12	I,12	10-17-11
SIO 63-368	31°06- 04.6'N	123°12.2- 07.5'W	III.6.63	37.0	26+25=51	XVII	11	I,11	13-17-12
SIO 58-161	26°53'N	115°00'W	VIII.24.58	62.0	26+25=51	XVIII	12	I,11	-

Morphometrics.—Morphometrics of a size series of larvae and early juveniles of *T. cuvieri* are presented in Table 21. A discussion comparing morphometrics of the three species of *Tetragonurus* is given in an earlier section titled "Comparative Morphometrics."

Ossification.—Meristics of a series of cleared and stained specimens are presented in Table 22. The principal caudal rays are first to develop with 4 + 4 rays ossified in a 9.1-mm specimen. A total complement of 9 + 8 principal caudal rays is attained by 10.9 mm. The second dorsal, anal, and pectoral fins are next to develop; all 12 second dorsal rays and 11 anal rays are ossified between 9.1 and 10.9 mm. A single anal spine is formed by 13.5 mm and a second, short anal spine is developed anterior to the first in a 65.0-mm juvenile. Twelve pectoral rays are present at 10.9 mm, and the full complement of 15 rays is formed by 13.5 mm.

Secondary caudal rays first appear at 10.9 mm, and form the full complement by 21.4 mm. The full complement of 15 spines in the first dorsal fin is present at 13.5 mm. Unfortunately, no specimens between 10.9 mm, which lacked dorsal spines, and 13.5 mm were available for staining to show a transition period in the early stages of the formation of the first dorsal fin. Bases of the pelvic fins are evident at 10.1 mm (Fig. 13D) and the full complement of I, 5 is developed by 14.0 mm.

The two anterior-most precaudal vertebrae have the neural spines ossified in a 7.6-mm specimen, and the full complement of 52 (26 + 26) vertebrae are formed in a 14.0-mm specimen.

Branchiostegal rays ossify early with 0 + 2 rays formed at 5.8 mm. The full set of 2 + 4 rays is developed at 7.6 mm. The variability in the number of branchiostegal rays in larger specimens (Table 22) is unusual for stromateoid fishes.

First arch gill rakers are first evident at 7.6 mm and increase to 5 + 1 + 8 in a 65.0-mm juvenile. The rakers on the lower limb develop quite early, but those on the upper limb are not completed until the juvenile stage (Table 22).

Preopercular spines develop along the margin of the preopercle and fewer, weaker spines lie embedded in the lower edge of the opercular flap. These spines are usually evident at about 10.0 mm, although one rather precocious 7.6-mm specimen has six spines along the preopercular margin; they gradually become embedded in the scaled opercle. Preopercular spines on *Tetragonurus* are heavier and more numerous than those found in nomeids, but less heavy than those developed on *Schedophilus*.

Premaxillary and dentary teeth first appear at 7.6 mm, and gradually increase in number with size. The dentary teeth are larger than those on the premaxillary, and are blade-like in shape. Dentition in *Tetragonurus* and other stromateoids is discussed in the introductory section of this paper.

Scales are first seen at 17.7 mm over the caudal peduncle, opercle, and along the midline of the body. By 21.4 mm, most of

Table 21. Morphometrics, in mm, of larvae of *Tetragonurus cuvieri* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
S6707-93.140	4.2 NL	2.4	0.48	0.24	0.10	0.42	-	-	-
"	5.2	3.0	.80	.32	.18	.52	-	-	-
S5603-110.80	5.2	3.1	.90	.30	.20	.56	-	-	-
B6207-90.80	6.6	4.2	1.5	.50	.42	1.2	-	-	-
B6207-90.120	7.6	4.6	1.9	.60	.54	1.4	base	base	-
Norpac 95 reg.	7.8	4.8	2.0	.68	.50	1.5	"	5.0	-
B6310-80.80	8.4	4.8	2.0	.66	.50	1.5	"	5.3	-
B5702-107.60	9.7	5.6	2.6	.76	.66	1.9	"	5.9	3.2
G6210-80.100	10.1	5.7	2.4	.80	.64	1.8	"	6.1	2.9
S5603-110.80	11.4 SL	6.6	2.8	.90	.68	2.3	"	6.9	3.6
Norpac 95 reg.	13.4	8.1	3.7	1.0	.84	2.8	5.0	8.4	4.7
Norpac 107 reg.	14.2	8.8	4.1	1.3	1.2	3.1	5.8	9.1	4.7
S6707-107.65	16.9	11.4	5.4	1.6	1.7	4.2	7.5	11.7	6.1
Norpac 95 reg.	17.4	11.0	4.5	1.4	1.3	3.7	7.2	11.4	5.9

the body is scaled except the abdominal region. By 65.0 mm, scales cover the entire body. With scales forming and the full complement of secondary caudal rays developed at 21.4 mm, the early juvenile period may be designated as beginning at about this size.

Pigmentation.—Larvae of *T. cuvieri* have pigment similar to *T. atlanticus* except that pigment is present at the tip of the tail in all stages of the former.

Yolk-sac larvae have continuous pigment along the ventral body margin from the head to the tip of the notochord; forward of the anus this line of pigment is over the gut (Fig. 13A). Pigment is on the dorsal margin only near the end of the notochord. Yolk-

Table 22. Meristics of cleared and stained larvae and juveniles of *Tetragonurus cuvieri* (specimen between dashed lines is undergoing notochord flexion)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
Norpac 95 reg.	5.0 NL	-	-	-	LP	-	-	-	-	-	-	-
"	5.8	-	-	-	LP	-	-	-	0+2	-	-	-
H4903-81.127	6.1	-	-	-	LP	-	-	-	0+3	-	-	-
Norpac 95 reg.	7.6	-	-	-	LP	-	-	2+ 0= 2†	2+4	0+1+6	3	2
H4903-81.127	8.9	-	-	-	LP	-	-	-	1+4	0+1+5	-	-
Loc. lost	9.1	-	Base	Base	LP	-	0-4+4-0	6+ 0= 6†	2+4	0+1+6	-	-
05701-100.60	10.9 SL	-	12	11	12	-	0-9+8-1	26+13=39†	2+4	1+1+7	4	8
G6301-80.80	13.5	XV	12	I,11	15	Base	0-9+8-3	27+21=48†	2+4	2+1+7	6	11
B5607-120.50	14.0	XVIII	12	I,11	17	I,5	3-9+8-3	26+26=52	2+4	2+1+8	9	12
Norpac 107 reg.	14.1	XVI	11	I,11	16	I,5	3-9+8-4	26+25=51	2+4	2+1+7	6	11
B6410-93.90	15.5	XVIII	12	I,12	15	I,3	3-9+8-4	26+26=52	2+4	1+1+7	7	10
S6707-90.120	16.0	XVII	13	I,11	14	I,3	4-9+8-4	26+26=52	2+4	2+1+7	11	15
Norpac 95 reg.	17.4	XV	13	I,12	15	I,3	4-9+8-4	26+26=52	2+4	2+1+8	10	13
S6707-107.65	17.7	XVI	12	I,11	15	I,5	6-9+8-6	26+26=52	2+4	1+1+8	11	18
J6607-93.80	18.7	XVIII	13	I,10	16	I,5	4-9+8-6	26+28=54	2+4	2+1+8	9	14
05611-93.55	21.4*	XVIII	12	I,12	15	I,5	10-9+8-9	26+26=52	1+4-R 1+4-L	4+1+7	13	18
C5412-107.40	65.0*	XVIII	12	II,11	15	I,5	11-9+8-11	27+26=53	2+4-R 2+3-L	5+1+8	15	24

* Juvenile

† Vertebrae not completely developed

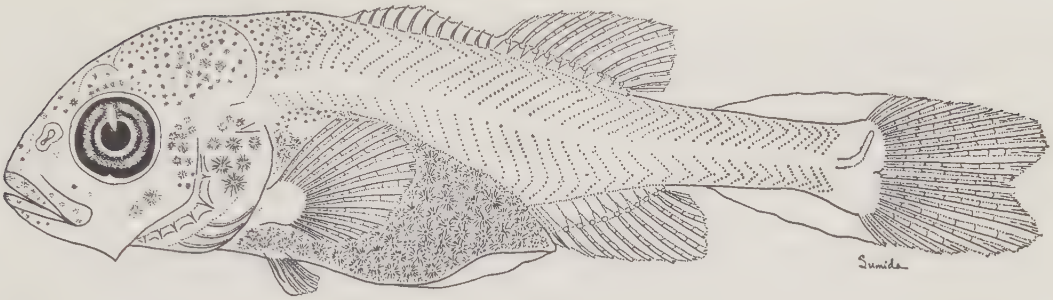


Figure 14. Postflexion larva of *Tetragonurus pacificus* (Tetragonuridae), 9.4 mm.

sac larvae can be distinguished from those of *T. atlanticus* by their larger size. *T. cuvieri* are 4.0 to 4.1 mm at hatching, whereas yolk-sac larvae of *T. atlanticus* measure 2.8 to 2.9 mm.

Preflexion larvae retain the same pigment as in the yolk-sac stage (Fig. 13B). Dorsal pigment extends forward in a double line (viewed from above) over the posteriormost 10 to 12 myomeres.

Flexion larvae add pigment on the head and along the lateral line (Fig. 13C). The eye bar forms in front of the eye at about 5.0 mm NL and behind the eye by about 6.0 mm; it persists through flexion. Pigment forms over the top of the head and spreads over the abdomen. Lateral line pigment forms from below the dorsal pigment forward to over the anus. By late flexion, 10.1 mm (Fig. 13D), the lateral line pigment is forming over the abdomen. Prominent dorsal pigment is developing behind the head and at the base of the developing second dorsal fin.

Postflexion larvae become pigmented over the entire head and body including the tail.

Tetragonurus pacificus
Abe, 1953
Figure 14

Literature.—Original descriptions of *Tetragonurus pacificus* were based on damaged specimens from the stomach of a yellowfin tuna caught west of the Solomon Islands at 6°36.5′S, 152°29′E (Abe, 1953). Grey (1955) reported a 9.5-mm specimen from Dana Station 3584 at 10°51.4′S, 168°40′W, and described a developmental series based principally on Indian Ocean material.

Material.—Three specimens were examined, one 19.5-mm juvenile from off Hawaii and two postflexion larvae from EASTROPAC station 30.055 at 3°47′N, 118°30′W.

Distribution.—Based on these two collections and the distribution given by Grey (1955), *T. pacificus* has a tropical distribution in the Pacific and Indian Ocean. It may be excluded from the oxygen minimum area of the eastern tropical Pacific as it was taken only at the western limit of the extensive EASTROPAC collections (Fig. 12).

Distinguishing Characters.—JUVENILES. *T. pacificus* is distinguished by the low number of vertebrae and of dorsal fin spines (Table 1).

LARVAE. Preflexion and postflexion larvae are distinguished by the low number of myomeres and by the pigmentation. Larvae of *T. pacificus* are the least pigmented among *Tetragonurus* and have no pigment on the body posterior to the termination of the gut until 13 mm. As Grey (1955) pointed out, larvae of *T. pacificus* develop fins and other structures at smaller sizes than either *T. atlanticus* or *T. cuvieri*.

Meristics.—Vertebrae 18 + 21 or 22 = 39 or 40; first dorsal XI or XII; second dorsal 10 or 11; anal I, 10 or 11; principal caudal rays 9 + 8; secondary caudal rays 11 dorsal + 11 ventral (Table 23).

Morphometrics.—Morphometrics of the three available specimens are presented in

Table 23. Meristics of postflexion larvae and a juvenile of *Tetragonurus pacificus* (Note: meristics of 19.5-mm specimen taken from radiograph; vertebral counts for 8.9-mm and 9.4-mm specimens are myomere counts)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 30.055	8.9 SL	XI	11	I,10	15	I,4	4-9+8-4	18+22=40	2+4	2+1+8	ca 4	ca 10
"	9.4	XI	11	I,10	16	I,4	4-9+8-4	18+22=40	2+4	3+1+8	4	11
Hawaii 70-9-2	19.5*	XII	10	I,11	18	I,5	11-9+8-11	18+21=39	2+4	5+1+10	13	ca 13

* Juvenile

Table 18 and body proportions in Table 10. A discussion of the morphometrics of the three species of *Tetragonurus* is presented in an earlier section.

Ossification.—Most of the major fins are developed on the 8.9-mm SL specimen of *T. pacificus* (Table 23), including the first dorsal (XI), second dorsal (11), anal (I, 10), pectoral (15), pelvic (I, 4), and caudal (4 + 17 + 4); only the caudal fin lacks the full complement of secondary rays and the pelvic fins are short one ray. All fins are complete between 9.4 and 19.5 mm.

Pigmentation.—One specimen of *T. pacificus*, a 9.4-mm postflexion larva, is illustrated (Fig. 14). Pigment is well developed over the head, nape, and abdomen, but the body is unpigmented behind the nape. Larvae of *T. pacificus* can be distinguished from *T. cuvieri* and *T. atlanticus* at all sizes by the lesser amount of pigment (Grey, 1955). The 19.5-mm juvenile is completely pigmented over the head and body, including the hypurals. Pigment is present on the membrane of the first dorsal fin and moderately at the bases of the second dorsal, anal, and caudal fins. The pelvic fins are lightly pigmented. The pectoral fin base is pigmented but not the rays.

Family NOMEIDAE

There are three genera in this family, *Nomeus*, *Cubiceps*, and *Psenes*, all widely distributed in the Pacific, Indian, and Atlantic oceans. Two of the fins in nomeids have the basic, unreduced counts for perciform fishes—pelvics I, 5 and caudal fin with 17 principal rays (15 branched). Secondary caudal rays range between 7 to 12 dorsal and 7 to 12 ventral. The first dorsal fin with (IX) X to XII spines is distinct from but contiguous with the second dorsal fin with I, 15 to 30 rays. The anal fin has II or III spines and 14 to 30 rays; the second dorsal and anal fins usually have about equal numbers of rays and seldom differ by more than ±2 rays. Pectoral fin counts range between 16 to 23.

The common vertebral count among species of nomeids is 31, with a range of (30) 31 to 42; the branchiostegal ray count is always 6 (2 + 4). The number of hypural bones supporting principal caudal rays in juveniles and adults is 2 + 2 (parhypural included); also present are 3 epurals and 3 predorsal bones, usually arranged 0/0/0 + 2/ (refer to introductory section dealing with predorsals). The first pterygiophore in the dorsal fin supports two spines in a secondary association for all nomeids except *Nomeus*, on which this pterygiophore secondarily supports a single spine. The anterior anal fin pterygiophore secondarily supports two spines for those species having three spines in this fin, but only a single spine is supported in a secondary association for species having two spines (i.e., *Cubiceps pauciradiatus*, *C. capensis*, *Psenes sio*, and *Nomeus gronovii*).

Upper jaw teeth on the premaxillary and lower jaw teeth on the palatine are arranged in a single row. Teeth on both jaws can be similar, i.e., needle-like, tapering, and often recurved; or the posterior dentary teeth can be blade-like, much as in *Tetragonurus*. The latter type of teeth is found only in *Psenes* (except *P. cyanophrys*). Teeth are present on the vomer, being limited to a patch on the head of the vomer in *Psenes* and *Nomeus*, but usually developed on the blade of the vomer in *Cubiceps*, with opposing tongue teeth. Palatine teeth are developed in a single row per side in all three genera.

All pelagic stromateoid fishes studied possess an air (swim) bladder in their larval and early juvenile stages. The air bladder can be observed in preflexion larvae soon after yolk absorption, e.g., by 2.5 mm in larvae of *Cubiceps pauciradiatus* and *Psenes sio*. The air bladder can readily be seen in all larger larvae, but it becomes obscured in juveniles by overlying musculature unless these specimens are cleared and stained. Horn (1975) discussed the importance of the swim bladder in larvae and juveniles of stromateoid fishes in maintaining hydrostatic equilibrium. Juvenile fishes swim in the surface layers, frequently in association with floating objects such as jellyfishes, where hovering and high maneuverability are essential components of their locomotor behavior.

Pelvic fins are the first fins to develop on larvae of *Psenes* and *Nomeus*. They form soon after yolk absorption on *Psenes* and become relatively large. Late larvae and early juveniles of these two genera have body pigment distributed in patches and bands, whereas it becomes uniformly distributed over the body on late preflexion larvae and early juveniles of the other genus *Cubiceps*. It is interesting to note that the early stages of *Psenes* and *Nomeus* are strongly associated with medusae, siphonophores or floating drift, whereas the juveniles of *Cubiceps* have only rarely been reported with medusae (Mansueti, 1963).

Genus *Cubiceps*

There is a minimum of seven species in the genus *Cubiceps*: the five species treated in this paper, *C. caeruleus*, *C. capensis*, *C. pauciradiatus*, *C.* sp. A, *C.* sp. B, and in addition, *C. gracilis* from the western Atlantic and Mediterranean and *C. squamiceps* (Lloyd, 1909) from the Indian Ocean. The two species simply designated *C.* sp. A and *C.* sp. B have a markedly higher caudal fin secondary ray count than the other five. Both may be undescribed, or one or both could belong to inadequately described nominal species.

Of the seven species considered valid, six have 31 vertebrae and only *C. gracilis* has a higher number of 33 or 34 vertebrae. All seven species have a modal first dorsal fin count of XI spines. The main difference in meristic counts are in the number of secondary caudal rays, in number of second dorsal and anal fin rays, and in the number of anal fin spines (Table 1). With regard to the latter, *C. pauciradiatus* and *C. capensis* have only two spines, whereas the other species have three. *C. capensis* also has the highest average counts of second dorsal and anal fin rays among the species of *Cubiceps*, whereas *C. pauciradiatus* has the lowest.

C. squamiceps has a lower second dorsal and anal fin ray count than *C. caeruleus*. A distinctive character of *C. caeruleus* is its vomerine teeth. A single longitudinal row of teeth is developed on the blade of the vomer and on the tongue (glossohyal) of *C. caeruleus*, whereas in *C. pauciradiatus*, *C. capensis* and *C. gracilis* the teeth occur in a large patch on these opposing bones.

Of the five species of *Cubiceps* collected in the eastern Pacific, three are known from two or three specimens each, i.e., *C. capensis*, *C.* sp. A and *C.* sp. B. *C. caeruleus* is fairly common at the equator and in the central water mass of the North Pacific, and *C. pauciradiatus* is both common and widely distributed in the tropical eastern Pacific.

Characters that can be used to distinguish between larvae and early juveniles of *Cubiceps* and *Psenes* are discussed in the introductory section under *Psenes*.

Morphometrics of *Cubiceps* species are discussed together in one comparative section.

Table 24. Body proportions of larvae and early juveniles of five species of *Cubiceps*, expressed as percentage of standard length (SL) or head length (HL)

Species and stage	Size range (mm)	Snout to anus/SL	Head length/SL	Eye diameter/HL	Snout length/HL	Depth at P base/SL	Sn-D/SL	Sn-A/SL	Sn-V/SL
Cubiceps caeruleus									
Preflexion	3.4- 4.4 NL	32-43	18-27	41-45	24-28	21-35	-	-	-
Flexion	4.6- 4.9 NL	42-56	27-36	41-45	23-32	34-43	42	48-57	-
Postflexion	4.7-22.7 SL*	49-62	31-36	41-48	18-27	38-46	39-44	54-63	39-41
Cubiceps pauciradiatus									
Preflexion	2.1- 3.8 NL	52-59	18-29	32-46	25-38	9-32	-	-	-
Flexion	3.7- 4.3 NL	58-62	32-35	32-34	25-27	35-37	40-43	58-62	-
Postflexion	4.4-27.5 SL	59-65	31-36	32-37	19-27	28-38	35-45	60-71	37-46
Cubiceps capensis									
Postflexion	13.9-15.7 SL	59-60	31-33	35-37	27-28	30-34	40-42	61-62	39
Cubiceps sp.A (Tropical)									
Postflexion	8.7-19.5 SL	55-57	33-34	36-40	19-23	36-42	41-47	57-60	36-38
Cubiceps sp.B (Central Water Mass)									
Postflexion	12.5-18.7 SL	56	31-34	37-39	21	38-39	38-41	57-58	35-37

*Postflexion may include both larvae and early juveniles

Comparative Morphometrics

Instead of devoting an individual section under each species of *Cubiceps* to a discussion of its shape and to changes that occur therein during development, the morphometrics of all five species will be compared in this section (Table 24).

Head Length.—The head length is proportionately shortest in early preflexion specimens, ca. 18% of NL, and increases to 28 or 29% of NL in late preflexion larvae. Subsequently (flexion, postflexion and early juveniles) head length ranges between 31 to 36% of SL for all five species of *Cubiceps*.

Eye Diameter.—The eye is proportionately larger on larvae of *C. caeruleus* (all stages) than on larvae of other kinds of *Cubiceps*. Eye diameter is 41 to 48% of HL on larvae of *C. caeruleus*. For flexion and postflexion specimens of *C. pauciradiatus*, eye diameter ranges between 32 to 37% of HL; for postflexion specimens of *C. capensis*, eye diameter is 35 to 37% of HL; for *Cubiceps* sp. A, 36 to 40% of HL; and for *Cubiceps* sp. B, 37 to 39% of HL.

Snout Length.—The snout is proportionately larger on preflexion specimens than on postflexion specimens of *C. pauciradiatus*. The range of Sn/HL on postflexion specimens of all five species is 18 to 28% of HL, with *C. capensis* at the top of the range.

Snout to Anus.—The distance from snout to anus is proportionately longer in *C. pauciradiatus*, 59 to 65% of SL on postflexion specimens, than on any other nomeid. On larvae of *C. caeruleus*, snout to anus lengths are only 32 to 43% of NL on early preflexion specimens, increasing to 42 to 56% of NL by late preflexion and ranging between 49 to 62% of SL on postflexion specimens, with most between 55 to 60% of SL. Postflexion specimens of the other three species of *Cubiceps* (*C. capensis*, *C.* sp. A, and *C.* sp. B) also have snout to anus lengths of between 55 to 60% of SL.

Body Depth at Pectoral Fin Base.—An extensive series of preflexion specimens were available for *C. pauciradiatus* and these strikingly show the increase in body depth that occurs during this stage. Newly hatched larvae are markedly more slender (9% of NL) than late stage preflexion larvae (32% of NL). The body depth at pectoral fin base is proportionately greatest during flexion, 3.7 to 4.3 mm NL, and early postflexion, 4.4 to 7.4 mm SL; during flexion it is 35 to 37% of NL, and on early postflexion specimens it is of similar proportions (36 to 38% of SL); on specimens 8.6 to 17.5 mm, body depth at pectoral fin base ranges between 32 to 36% of SL, decreasing to 28 to 30% of SL on the two larger specimens in the series (22.2 and 27.5 mm). Preflexion specimens of *C. caeruleus* between 3.4 to 4.4 mm show an increase in body depth at pectoral fin base from 21 to 35% of NL (specimens smaller than 3.4 mm were not available); flexion specimens have a body depth at pectoral fin base of 34 to 43% of NL, and postflexion specimens of 38 to 46% of SL. Specimens of *C. caeruleus* are deeper bodied over the range of sizes studied (3.4 to 22.7 mm) than are specimens of *C. pauciradiatus* of similar sizes. The two specimens of *C. capensis* (13.9 and 15.7 mm SL) are as slender as comparable-sized specimens of *C. pauciradiatus* (30 to 34% of SL). The other two species are intermediate in this dimension between *C. pauciradiatus* and *C. caeruleus*.

In the following paragraphs the proportionate length of fin origins will be considered only for postflexion specimens of *Cubiceps*.

Snout to Dorsal Fin Origin.—As noted under the discussion of morphometric measurements for *Psenes*, the origin of the first dorsal fin is farther forward in *Psenes*, Sn/D lengths ranging between 27 to 40% of SL, while in *Cubiceps* these range between 35 to 47% of SL. Among *Cubiceps*, this proportionate measurement is not markedly different for the five species.

Snout to Anal Fin Origin.—The anal fin origin is close to the anus, seldom separated by more than 2 to 4% of SL. Consequently, the proportionate lengths from snout to anal fin origin are similar to those for snout to anus. This distance is proportionately longest in *C. pauciradiatus* (60 to 71% of SL), and shortest in *Cubiceps* sp. B (57 to 58% of SL).

Snout to Insertion of Pelvic Fins.—The insertions of the pelvic fins are either immediately under the dorsal fin origin, slightly forward of it, or slightly behind it. Only in *C. pauciradiatus* is the pelvic fin insertion consistently behind the first dorsal fin origin.

Comparative Pigmentation

Early stage larvae are available for only two species of *Cubiceps*: *C. caeruleus* and *C. pauciradiatus*; for the three other species taken in the eastern Pacific we have late postflexion larvae and/or early juveniles. Hence the discussion of pigment on preflexion and flexion stage larvae of *Cubiceps* must be limited to the former two species.

The most striking difference in the pigment patterns of early stage larvae of *C. caeruleus* and *C. pauciradiatus* is the presence of a line of pigment spots along the ventral midline of the tail on preflexion, flexion, and early postflexion larvae of *C. caeruleus* (gone by 6.2 mm), and its absence on post-yolk-sac and further developed larvae of *C. pauciradiatus*. Contrastingly, preflexion and later stage larvae of *C. pauciradiatus* have opposing dorsal, ventral and lateral line pigment patches on the tail about midway between the anus and the notochord tip. This type of tail pigment is lacking on larvae of *C. caeruleus*.

Neither of the above types of tail pigment is unique to *Cubiceps* among nomeids. Four of the five species of *Psenes* have the ventral midline series of pigment spots on preflexion larvae, persisting until the early postflexion stage (lacking on *P. cyanophrys*); all five species of *Psenes* have mid-tail lateral-line pigment extending over several myomeres with opposing ventral and usually dorsal patches, such as on *C. pauciradiatus*. On flexion and postflexion larvae, all five species of *Psenes* have a pigment patch over the hypural plates that is lacking on *Cubiceps* larvae. Preflexion larvae of *Psenes* and *Cubiceps* are most readily separable by the presence of early-forming pelvic fins on *Psenes* and their absence on *Cubiceps*. Also, pigment forms on top of the head in later preflexion larvae of *Cubiceps*, whereas it is lacking on the head of preflexion larvae of *Psenes* beyond the yolk-sac stage, only to appear later during flexion or early postflexion.

Sparta (1946) described the early life history stages of *Cubiceps gracilis* Lowe. The smallest specimen illustrated, a late preflexion specimen, lacks the series of ventral midline melanophores on the tail portion of the body that is found on *C. caeruleus*, but has a series of four or five spots along the outer margin of the anlage of the caudal fin, and has the head and abdomen more heavily pigmented than on comparable stages of *C. caeruleus* or *C. pauciradiatus*. On postflexion specimens, pigment spreads posteriad from the head on to the nape of the trunk, and also from a center of pigmentation on the tail, much as in *C. caeruleus*.

Nellen (1973) illustrated an 8.8-mm TL larva of a nomeid, as that of *Psenes whiteleggii*. The top of the head, opercle and abdomen are heavily pigmented; pigment on the body is limited to a series of ventral pigment spots and two spots over the inferior hypurals. The pigment pattern is closest to *C. caeruleus*. He sent us photographs of several additional specimens. Preflexion larvae lack precocious pelvic fins. We have no hesitation in assigning the larvae to *Cubiceps*, with the strong possibility that they belong to *C. squamiceps*.

The five species of *Cubiceps* become rather uniformly pigmented over the head and body on late postflexion larvae or early juveniles. There is no clustering of pigment into patches or bands as is the case on early juveniles of *Psenes* and *Nomeus*. As will be discussed in the species accounts, the pattern of pigment augmentation is somewhat different for each species.

On postflexion larvae of *C. caeruleus*, the pigment spreads posteriad from the head onto the trunk, while a lateral pigment patch forms simultaneously on the tail at about myomeres 18 to 22 and spreads in all directions. The pigment soon fills in from the head to the caudal peduncle, with the latter area the last to become pigmented.

The opposing dorsal, lateral line, and ventral pigment patches are a conspicuous feature on the body of *C. pauciradiatus* larvae and become a primary center for pigment augmentation on postflexion larvae. However, pigment forms along the length of the dorsal and ventral margins of the body except on the caudal peduncle before spreading over the body itself. The upper half of the body above the lateral line becomes rather uniformly pigmented except for the caudal peduncle by 8.6 mm; the latter becomes gradually pigmented in larger sizes.

Although additional material of *C. capensis* is needed to establish the sequence of pigment augmentation in this species, the 15.7-mm specimen is pigmented similarly to similar-sized specimens of *C. pauciradiatus*.

Pigment forms earlier on *C.* sp. A than on other species of *Cubiceps*, inasmuch as the 8.7-mm specimen is quite heavily pigmented over the head and body except along the bases of the dorsal, anal, and caudal fins.

Pigment augmentation appears to be closely allied in *C. caeruleus* and *C.* sp. B in that pigment first forms heavily over the head, abdomen and nape and only later over the tail portion of the body. However, tail pigment forms earlier on *C. caeruleus* than on *C.* sp. B.

It is probable that differences in pigment patterns in early juveniles of *Cubiceps* and *Psenes* may be associated with different behavioral patterns. Stromateoid fishes associated with jellyfishes or floating debris, of which *Psenes* is a prime example, usually have conspicuous patches or streaks of pigment on their bodies as early juveniles, but later become rather uniformly pigmented over their bodies when they become deeper living fish. We assume that *Cubiceps*, with its drab pigment patterns, is seldom associated with floating objects, but rather settles to deeper levels as early juveniles. Horn (1975) has emphasized the importance of coloration and maneuverability to the juvenile stromateoid that accumulates beneath floating objects, especially coelenterates. He notes that the young fish typically have a banded, mottled, or blotched pattern whereas adults are generally uniform in color or are dark above and pale below; also, the duration of the juvenile color pattern is similar to the period when the fishes are associated with floating objects. Our observations reinforce those of Horn.

Cubiceps caeruleus
Regan, 1914
Figures 15 and 16

Literature.—*Cubiceps caeruleus* was reported from the eastern Pacific by Haedrich and Nielsen (1966) and Parin (1968). Specimens assigned to *C. gracilis* from Japan (Abe, 1955b) were reassigned to this species by Haedrich (1972) on the basis of their teeth. This species was originally described by Regan (1914) from off Three Kings Island in the Tasman Sea.

Material.—Extensive collections of larvae were examined from EASTROPAC material. Juveniles collected by STOR cruises in the same area, and larvae and juveniles collected near Hawaii were also examined.

Distribution.—*Cubiceps caeruleus* is widely distributed in the eastern tropical Pacific (Fig. 17), although more abundant offshore. It is also found over an extensive area between ca. 20° and 32°N and 123° to 180°W (Fig. 18). In this region, it would be classed as a central water mass species. It appears to avoid the oxygen minimum waters off the coasts of central America and Mexico, and does not occur in the Gulf of California. However, the offshore distribution obtained on EASTROPAC cruises is contiguous with the distribution obtained on CalCOFI cruises including NORPAC. This is the only species of stromateoid fishes for which there is such a distinct continuation in distributions as between EASTROPAC and CalCOFI cruises.

Distinguishing Characters.—Fin meristics and dentition are distinctive in *C. caeruleus* juveniles. The dorsal fin meristics of X to XII, I, 20 to 23 in combination with the anal fin meristics of III, 20 to 22 and only 7 to 10 secondary caudal rays are characteristic for the species. In addition, the teeth on the blade of the vomer are in a single row, not in patches as in *C. pauciradiatus*, *C. capensis* or *C. gracilis*.

LARVAE. The pigment pattern and lack of precocious pelvic fins will easily distinguish preflexion larvae of *C. caeruleus* from other nomeids. The pattern of pigment augmentation in flexion and postflexion larvae is strikingly different from *C. pauciradiatus* or any species of *Psenes*. Pigmentation in *C. caeruleus* is described in a subsequent section, and was also discussed above under "Comparative Pigmentation."

Meristics.—Vertebrae 12 + 19 = 31; first dorsal X or XI, rarely XII (average 10.9); second dorsal I, 20 to 23 (average I, 21.1); anal III, 20 to 22 (average III, 20.6); principal caudal rays 9 + 8; secondary caudal rays 7 to 10 dorsal + 7 to 10 ventral (average 8.5 + 8.6).

Meristics of 25 specimens from about 4°S to about 31°N and from about 96°W to about 158°W are given in Table 25. No geographical variation of any count is indicated.

Morphometrics.—Morphometrics of a size series of *C. caeruleus* are presented in Table 26 and body proportions are presented in Table 24. A discussion of the morphometrics of *C. caeruleus* in relation to other *Cubiceps* species is given in an earlier section titled "Comparative Morphometrics."

Ossification.—Fin ray development first begins in the caudal fin. A 4.8-mm specimen has 3 + 3 principal caudal rays developed, and the full complement of 9 + 8 principal caudal rays is achieved by 6.5 mm (Table 27). The anal, second dorsal, and pectoral fin rays begin to develop by 5.2 mm. The second dorsal fin is complete and the anal fin nearly complete in a 6.5-mm specimen, but the pectoral fins add rays until about 10.7 mm. The first dorsal and pelvic fins have a brief development period following notochord flexion, and rapidly achieve their full count of rays by 6.5 mm and 7.1

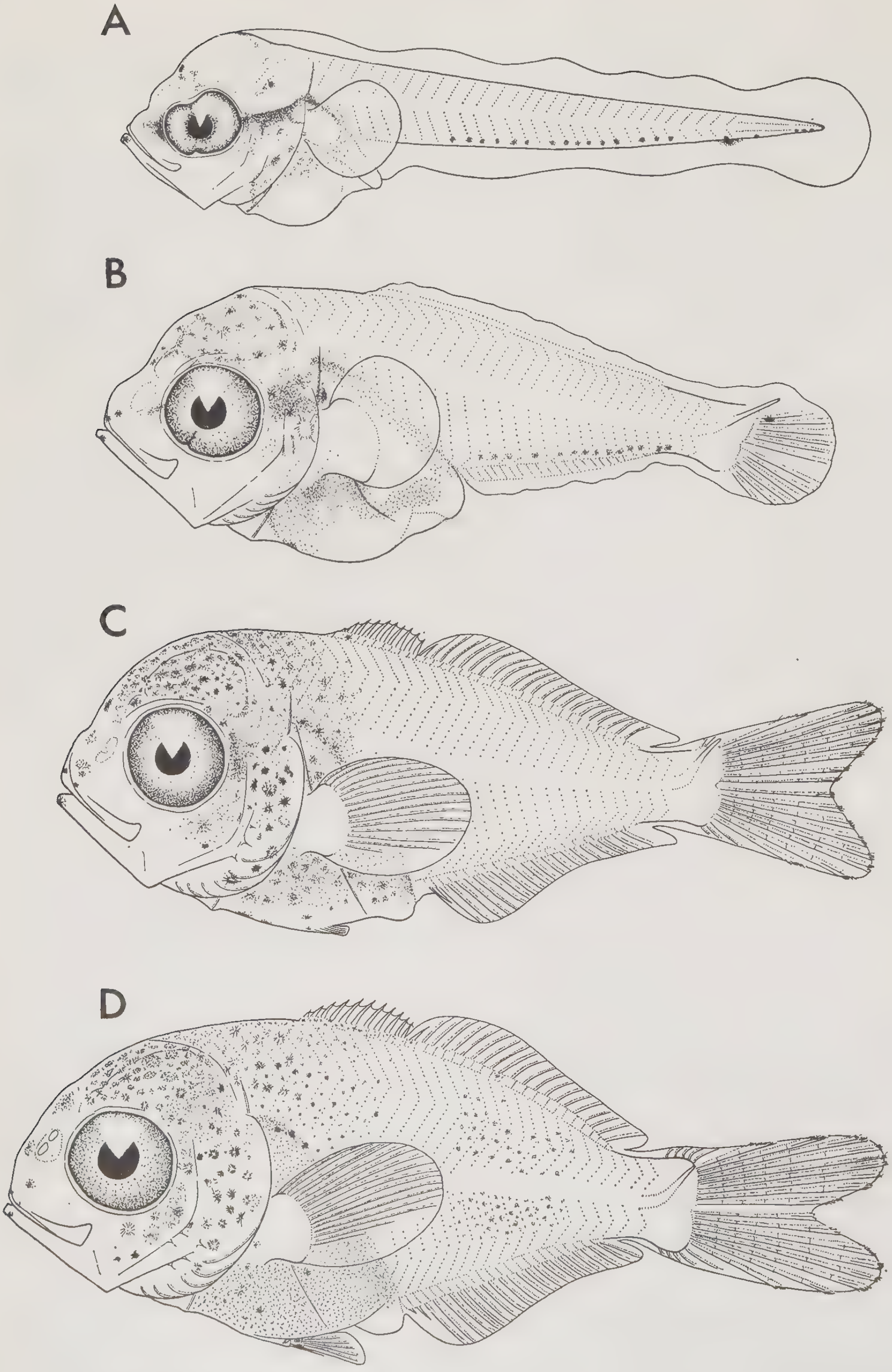


Figure 15. Developmental stages of *Cubiceps caeruleus* (Nomeidae). A—3.7-mm preflexion larva; B—4.6-mm flexion larva; C—6.2-mm postflexion larva; D—7.1-mm postflexion larva.

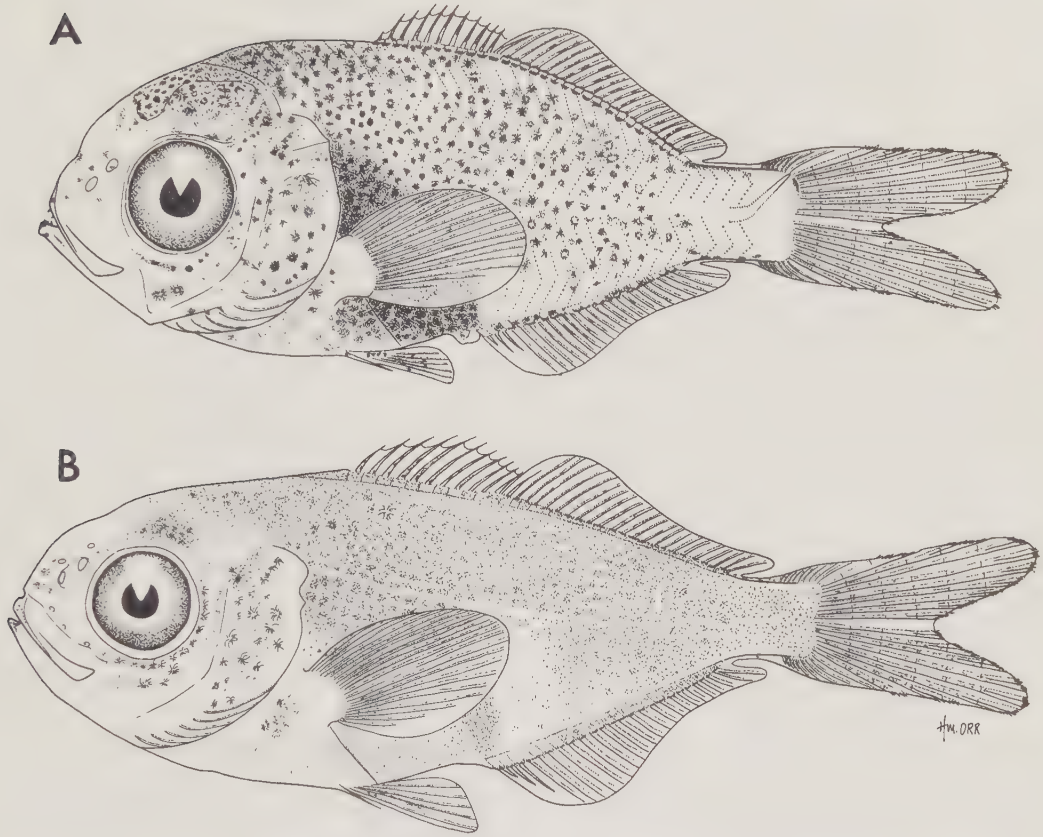


Figure 16. Developmental stages of *Cubiceps caeruleus* (Nomeidae). A—9.4-mm postflexion larva; B—17.5-mm early juvenile.

mm, respectively. Secondary caudal rays are first observed on a 6.5-mm specimen with 4 + 4 rays and may be complete on a 10.0-mm specimen, with 8 + 8 rays.

The vertebral column ossifies early with a 4.4-mm specimen having four neural spines of the most anterior precaudal vertebrae formed, but not their centra. All 31 (12 + 19) vertebrae are ossified by 6.5 mm.

Branchiostegal rays are completely formed in a 4.4-mm specimen. Gill rakers first appear at 5.2 mm, and the full count is reached in a 26.4-mm specimen.

Two or three small, inconspicuous spines form along the preopercular margin by 5.2 mm, and also along the more anterior preopercular ridge by 7.1 mm. These weak spines do not persist very long during the larval period and are gradually resorbed beginning in a 10.7-mm specimen, with no trace left in a 16.0-mm specimen.

A few dentary teeth appear on an 8.0-mm specimen, and premaxillary teeth as well on a 10.0-mm specimen. The teeth in both jaws are small and conical. Two palatine teeth are formed on a 17.0-mm specimen, but teeth are lacking on the vomer and glossohyal through the 26.4-mm specimen in the cleared and stained series.

Scale formation in *C. caeruleus* occurs early at a relatively small size. A 10.7-mm specimen has most of its body covered with scales which are very deciduous at this stage. This specimen also has the complete count

Table 25. Meristics of 25 juveniles of *Cubiceps caeruleus* selected from over its distributional range in the eastern Pacific, including off Hawaii (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
J7210-31.135	31°00'N	135°00'W	X.1.72	16.0	12+19=31	XI	I,23	III,20	8-17-8
J7210-31.145	31°00'N	145°00'W	X.4.72	12.5	12+19=31	XI	I,21	III,20	9-17-9
J7210-24.131	24°00'N	131°00'W	X.26.72	16.5	12+19=31	XI	I,21	III,21	9-17-9
J7205-24.145	24°00'N	145°00'W	V.22.72	23.0	12+19=31	XI	I,21	III,21	9-17-9
T.C. 32.010	21°22'N	158°15'W	VII.15.67	63.0	12+19=31	XI	I,22	III,20	9-17-9
T.C. 32.007	21°23'N	158°15'W	VII.14.67	68.0	12+19=31	XI	I,22	III,21	10-17-10
T.C. 32.016	21°19'N	158°13'W	VII.19.67	71.0	12+19=31	XII	I,21	III,20	8-17-10
T.C. 32.020	21°00'N	158°29'W	VII.21.67	65.0	12+19=31	XI	I,21	III,20	9-17-10
J7210-20.123	20°00'N	123°00'W	XI.6.72	15.5	12+19=31	XI	I,20	III,21	9-17-9
"	"	"	"	17.5	12+19=31	XI	I,21	III,21	9-17-9
T.C. 51.070	03°02'S	120°59'W	XI.13.70	31.0	12+19=31	XI	I,21	III,20	8-17-8
"	"	"	"	51.0	12+19=31	XI	I,22	III,21	9-17-8
T.C. 51.071	03°12'S	121°27'W	XI.14.70	35.0	12+19=31	XI	I,21	III,22	9-17-9
"	"	"	"	57.0	12+19=31	XI	I,21	III,21	8-17-8
T.C. 51.056	03°15'S	119°10'W	XI.10.70	25.0	12+19=31	XI	I,22	III,20	8-17-8
"	"	"	"	35.5	12+19=31	XI	I,21	III,20	8-17-8
T.C. 51.065	03°29'S	120°14'W	XI.12.70	24.5	12+19=31	XI	I,21	III,20	8-17-8
T.C. 51.063	03°44'S	119°30'W	XI.12.70	46.0	12+19=31	XI	I,20	III,20	8-17-8
"	"	"	"	54.0	12+19=31	XI	I,20	III,21	8-17-8
Jord. 65.144	04°00.5'S	97°02'W	IX.9.71	121.0	12+19=31	XI	I,21	III,21	8-17-8
"	"	"	"	133.0	12+19=31	XI	I,21	III,20	9-17-9
T.C. 51.048	04°02.5'S	118°48'W	XI.8.70	46.0	12+19=31	XI	I,21	III,21	9-17-8
"	"	"	"	48.0	12+19=31	XI	I,20	III,21	9-17-8
Jord. 65.138	04°05.2'S	96°31'W	IX.7.71	112.0	12+19=31	XI	I,21	III,21	7-17-7
"	"	"	"	125.0	12+19=31	X	I,21	III,21	9-17-9

of rays in all fins, hence may be considered a juvenile.

Pigmentation.—Preflexion larvae of *C. caeruleus* (2.8 to 4.3 mm) are pigmented in three major areas: the ventral tail margin, over the abdominal wall, and on the head. A 3.7-mm preflexion larva (Fig. 15A) shows this characteristic pigment pattern. The ventral tail pigment consists of a row of about 15 discrete melanophores spaced along the tail margin, usually one per myomere with a cluster near the tip of the tail. Abdominal pigment is initially heaviest on the dorsal wall of the peritoneum and gradually spreads out laterally. Head pigment is found on the tips of both jaws, over the midbrain, and in a conspicuous bar extending through the midline of the eyes.

Pigment intensifies over the head and abdomen on flexion larvae of 4.6 to 5.1 mm (Fig. 15B). However, by late flexion, the pigment bar through the eyes is faint and the row of ventral tail melanophores are less conspicuous.

By 6.2 mm (Fig. 15C), postflexion larvae lose the ventral row of melanophores and the pigment bar through the eyes. Pigment covers the abdomen and also begins to spread over the shoulder. Beginning at about 6.6 mm, an aggregation of pigment appears on the body at about myomeres 18 to 22, which spreads to myomeres 17 to 25 by 7.1 mm (Fig. 15D). Pigment progressively fills in the area between the shoulder and posterior part of the trunk so that by 9.4 mm (Fig. 16A) the body is covered with pigment except for the caudal peduncle, a small area behind the lower abdomen and the forward part of the head. The region of the caudal peduncle remains unpigmented except along the dorsal and ventral margins until about 15 mm when the early juveniles are fairly uniformly pigmented. However, as seen in the 17.5-mm specimen (Fig. 16B), the ventral area anterior and posterior to

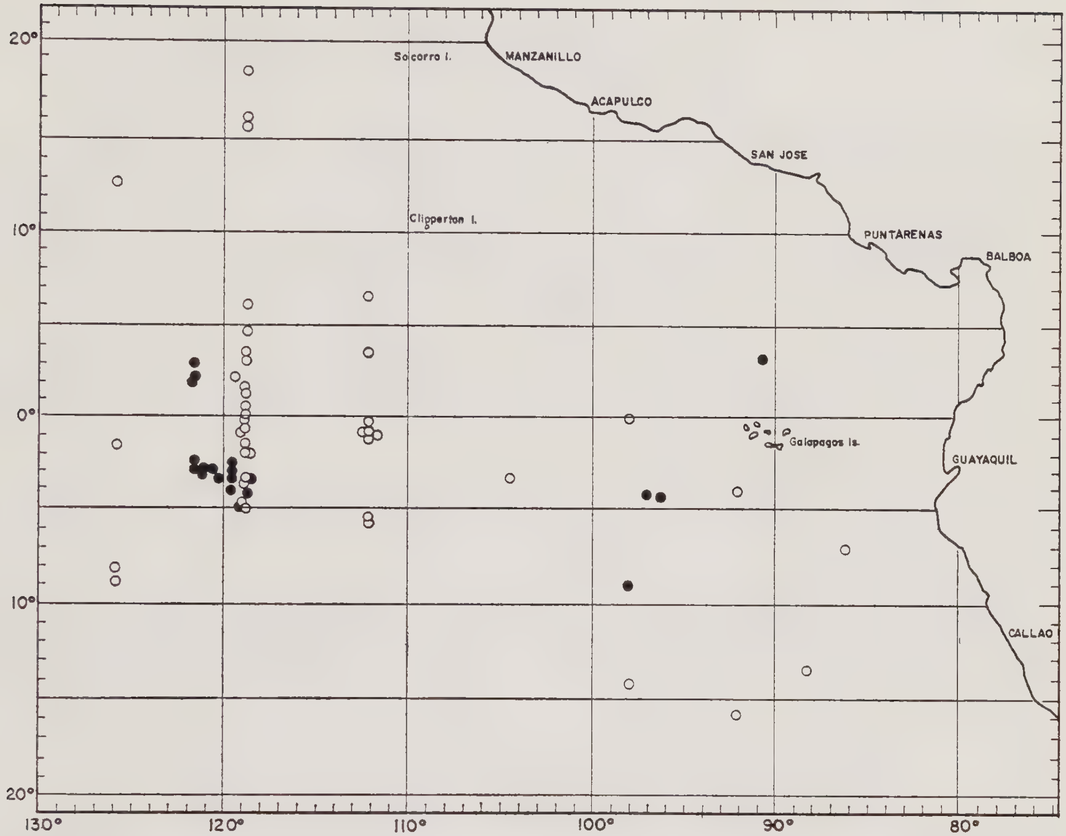


Figure 17. Occurrences of *Cubiceps caeruleus* larvae (open circles) and juveniles (closed circles) in the eastern tropical Pacific.

the abdomen and the lower portion of the head remain sparsely pigmented.

Cubiceps capensis
(Smith, 1849)
Figure 19

Literature.—Craddock and Mead (1970) reported taking a 139-mm specimen at 33°50.5′S, 82°06.14′ W.

Material.—Two late postflexion or early juvenile specimens, 13.9 mm and 15.7 mm, were studied from the eastern South Pacific. In addition, radiographs were studied from Indian Ocean and South African specimens.

Distribution.—*C. capensis* is circumglobal in distribution in the southern oceans. In the South Pacific, it is a temperate water species. Our two specimens are from widely separated localities, one from the offshore central water mass obtained on SIO cruise CATO II at 25°14.8′S, 155°07.7′W, the other taken on SIO expedition STEP 1 off Chile at 18°06′S, 80°56′W. The specimen reported by Craddock and Mead (1970) also was taken off Chile.

Distinguishing Characters of Juveniles.—The second dorsal (I, 25) and anal (II, 22 or 23) fin meristics are distinctive for *C. capensis* juveniles. These are the highest counts for a species of *Cubiceps*. The arrangement of predorsal bones differs from all other *Cubiceps* except *C. gracilis* (see following section on ossification). The latter

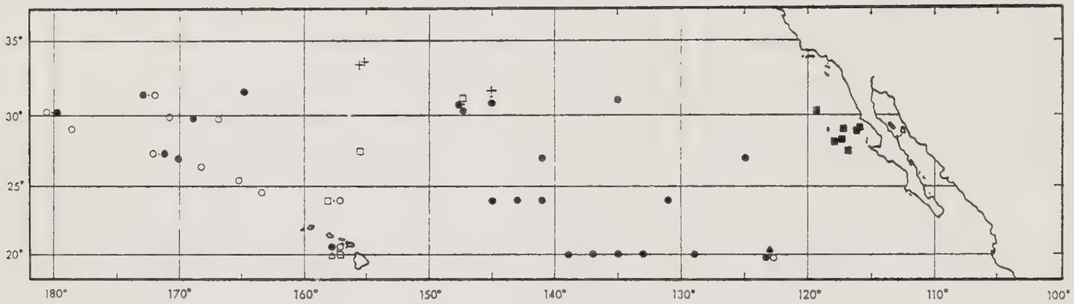


Figure 18. Occurrences of three species of *Cubiceps* and four species of *Psenes* on regular CalCOFI cruises, extended CalCOFI cruises 7205 and 7210, and NORPAC Expedition. *Cubiceps caeruleus* indicated by closed circles, *C. pauciradiatus* by open circles, *C.* sp. B by "plus" signs, *Psenes arafurensis* by open squares, *P. cyanophrys* by an open triangle, *P. maculatus* by a closed triangle, and *P. pellucidus* by solid squares. (Dots indicate station locations.)

species has 33 or 34 vertebrae, not 31, as in other *Cubiceps*.

Meristics.—Vertebrae 12 + 19 = 31; first dorsal X or XI; second dorsal I, 25; anal II, 22 or 23; principal caudal rays 9 + 8; secondary caudal rays 8 or 9 dorsal + 8 or 9 ventral (see Table 28).

Morphometrics.—The morphometrics of the two specimens of *C. capensis* are given in Table 29, and their body proportions

Table 26. Morphometrics, in mm, of larvae and juveniles of *Cubiceps caeruleus* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 60.072	3.4 NL	1.1	0.62	0.27	0.15	0.70	-	-	-
ETP 60.078	3.7	1.3	0.92	0.38	0.26	0.96	-	-	-
ETP 45.125	4.4	1.9	1.2	0.54	0.30	1.6	base	2.2	-
ETP 50.071	4.8	2.2	1.3	0.58	0.42	1.7	"	2.4	-
ETP 50.061	4.9	2.1	1.4	0.56	0.34	1.7	"	2.4	-
ETP 30.083	4.6	2.5	1.6	0.68	0.36	1.9	1.9	2.5	-
ETP 45.177	4.9	2.4	1.5	0.68	0.40	2.0	2.0	2.5	2.0
ETP 75.064	4.7 SL	2.4	1.6	0.68	0.42	1.9	2.0	2.7	2.0
ETP 50.082	5.2	2.5	1.6	0.66	0.44	2.0	2.1	2.8	2.0
ETP 50.071	6.2	3.2	2.1	0.88	0.56	2.6	2.5	3.5	2.4
"	6.5	3.6	2.4	1.0	0.50	2.9	2.9	4.0	2.7
"	7.1	3.9	2.4	1.0	0.58	3.2	2.9	4.2	3.1
ETP 50.055	8.0	4.8	2.8	1.1	0.55	3.6	3.5	4.8	3.3
ETP 60.060	10.0	6.2	3.4	1.4	0.60	4.4	4.2	6.3	4.3
ETP 12.221	10.1	6.0	3.6	1.5	0.84	4.5	4.2	6.1	4.2
J7210-20.123	11.2*	6.4	3.7	1.6	0.97	4.4	4.5	6.5	4.3
"	12.4*	7.0	4.4	1.8	0.97	5.4	5.0	7.3	5.2
South Tow 13	13.2*	7.6	4.4	2.1	0.92	5.6	5.4	8.0	5.5
J7205-20.129	14.4*	8.5	4.6	2.1	0.94	5.8	5.7	8.6	5.6
"	15.0*	8.9	5.0	2.1	1.3	5.9	6.0	9.1	6.0
J7210-31.135	16.0*	9.1	5.3	2.2	1.3	6.2	6.2	9.3	6.4
ETP 45.177	17.0*	9.8	6.0	2.3	1.4	6.9	6.8	10.7	6.5
J7205-20.129	22.7*	12.5	7.2	2.7	1.5	8.5	9.2	13.2	8.0

* Juvenile

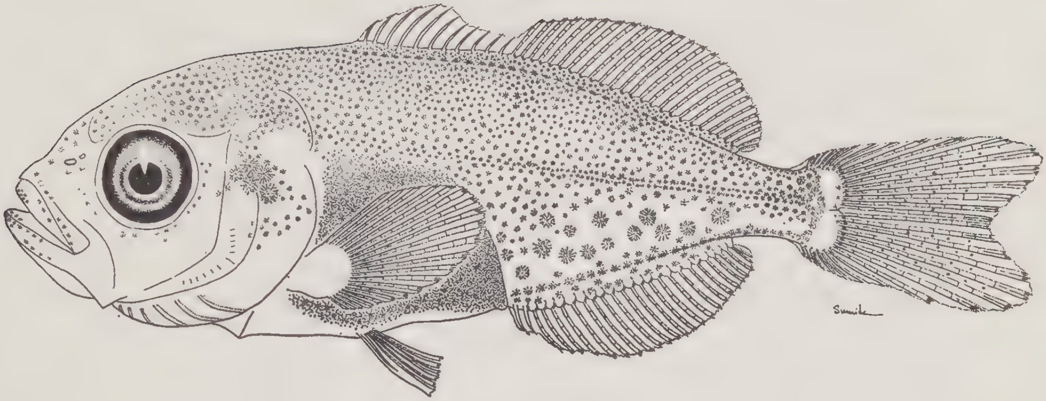


Figure 19. Early juvenile of *Cubiceps capensis* (Nomeidae), 15.7 mm.

in Table 24, and these are discussed in the previous "Comparative Morphometrics" section.

Ossification.—Although no specimen was cleared and stained, the arrangement of predorsal bones and pterygiophores in relation to the axial skeleton was determined from radiographs of these and additional specimens. The number of precaudal vertebrae could be readily determined on the two small specimens as 12. Separation of vertebrae into precaudal versus caudal groups becomes difficult on larger specimens. The dorsal fin is preceded by three predorsal bones. The first predorsal precedes the first neural

Table 27. Meristics of cleared and stained larvae and juveniles of *Cubiceps caeruleus* (specimen between dashed lines is undergoing notochord flexion)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 45.125	4.4 NL	-	-	-	LP	-	-	4+ 0= 4 †	2+4	-	-	-
ETP 50.071	4.8	-	-	-	LP	-	0-3+3-0	5+ 0= 5 †	2+4	-	-	-
ETP 50.082	5.2 SL	-	6	6	8	-	0-8+8-0	12+11=23 †	2+4	0+1+6	-	-
ETP 50.071	6.5	X	I,21	II,22	16	I,4	4-9+8-4	12+19=31	2+4	1+1+9	-	-
ETP 75.068	7.1	X	I,21	III,20	16	I,5	4-9+8-5	12+19=31	2+4	2+1+9	-	-
ETP 50.055	8.0	XI	I,22	III,21	17	I,5	6-9+8-6	12+19=31	2+4	3+1+11	0	2
ETP 60.060	10.0	XI	I,21	III,21	19	I,5	8-9+8-8	12+19=31	2+4	4+1+12	2	4
J7210-20.123	10.7*	XI	I,20	III,20	20	I,5	8-9+8-8	12+19=31	2+4	6+1+12	1	3
"	12.4*	XI	I,21	III,22	21	I,5	9-9+8-9	12+19=31	2+4	6+1+13	6	5
Hawaii 71-6-14	13.7*	XI	I,22	III,20	20	I,5	9-9+8-10	12+19=31	2+4	6+1+14	6	6
J7205-20.129	14.4*	XI	I,22	III,20	22	I,5	10-9+8-10	12+19=31	2+4	7+1+15	6	4
T.C. 51.066	15.2*	XI	I,20	III,21	21	I,5	8-9+8-8	12+19=31	2+4	5+1+15	4	6
J7210-31.145	16.0*	XI	I,22	III,20	23	I,5	9-9+8-9	12+19=31	2+4	5+1+15	5	4
ETP 45.177	17.0*	X	I,22	III,21	22	I,5	7-9+8-8	12+19=31	2+4	6+1+14	7	6
T.C. 51.066	18.2*	X	I,22	III,21	22	I,5	9-9+8-9	12+19=31	2+4	7+1+15	8	5
T.C. 51.066	20.2*	XI	I,20	III,21	21	I,5	8-9+8-8	12+19=31	2+4	7+1+15	6	5
J7210-20.123	21.2*	XI	I,20	III,21	21	I,5	9-9+8-9	12+19=31	2+4	7+1+14	9	8
T.C. 51.066	26.4*	XI	I,21	III,20	22	I,5	8-9+8-8	12+19=31	2+4	8+1+16	10	9

* Juvenile

† Vertebrae not completely developed

Table 28. Meristics of juveniles of *Cubiceps capensis*, *Cubiceps* sp. A, and *Cubiceps* sp. B (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Cubiceps capensis									
Step 1-32	18°06'S	80°56'W	X.31.60	13.9	12+19=31	XI	I,25	II,22	9-17-9
Cato II-B3.119	25°14.8'S	155°07.7'W	VIII.1.72	15.7	12+19=31	X	I,25	II,23	8-17-8
Cubiceps sp.A									
ETP 11.068 *	06°05'N	118°51'W	II.3.67	8.7	12+19=31	XI	I,22	III,21	mangled
T.C. 51.081	02°10'N	121°37'W	XI.18.70	14.0	12+19=31	XI	I,23	III,22	12-17-12
Jord. 60.150	09°27.7'N	117°49'W	IV.7.71	19.5	12+19=31	XI	I,22	III,22	12-17-12
Cubiceps sp.B									
J7210-31.145	31°00'N	145°00'W	X.4.72	12.5	12+19=31	XI	I,20	III,20	12-17-12
Aries 9-H17	27°28.2-27.0'N	155°28.6-47.0'W	X.2.71	17.9	12+19=31	XI	I,20	III,20	11-17-12
Aries 9-A2	27°22.4-11.8'N	155°01.2-02.9'W	IX.24.71	18.7	12+19=31	XI	I,19	III,20	12-17-12

* Probably postflexion larval stage

spine, the second is spaced between the first and second neural spines, and the third predorsal is spaced between the second and third neural spines, but is not accompanied by the first dorsal fin pterygiophore as in most nomeids; rather this pterygiophore is spaced between the third and fourth neural spines, similar in arrangement to *Cubiceps gracilis*. (The first dorsal pterygiophore supports two spines in a secondary association and the first anal pterygiophore supports only one spine secondarily.) The spacing of anal fin pterygiophores in relation to haemal spines is given in Table 3.

Pigmentation.—The 13.9-mm specimen is bleached and thus of no value for observation of pigmentation. The 15.7-mm specimen (Fig. 19) has well-preserved pigment. It is uniformly pigmented over the dorsal half of the body and more sparsely pigmented on the ventral half; however, pigment is almost lacking over the hypural bones. Pigment is heavy on the upper part of the head, is present on the lips of both upper and lower jaws, but is sparse on the head ventral to the eyes. An accentuated line of pigment spots is present just below the length of the two dorsal fins and anal fin along the margins of the body. Pigment is developed along the base of the caudal fin, with a sprinkling of pigment over the caudal fin. None of the other fins is pigmented.

Cubiceps pauciradiatus
Günther, 1872
Figures 20 and 21

Literature.—Previous records for the eastern Pacific by Alverson (1963) and Haedrich and Nielsen (1966) have referred to *C. carinatus* Nichols and Murphy (1944), which was described from two specimens obtained from approximately 180 miles southwest, 5° west of Cape Mala, Panama. *Cubiceps carinatus* is here considered a junior synonym of *C. pauciradiatus* for reasons discussed below. Abe (1959) reports a specimen from off Japan.

Material.—Extensive collections of larvae were examined from EASTROPAC cruises, from collections by T. Clarke off Hawaii, and from CalCOFI cruises. Juvenile and adult material was examined from R/V DAVID STARR JORDAN and R/V TOWNSEND CROMWELL cruises in the eastern tropical Pacific and from TOWNSEND CROMWELL cruise 32 off Hawaii. Comparative larval material was examined from the Atlantic, Indian, and west Pacific oceans. Radiographs of the type and paratype of *C. carinatus* were made available by the American Museum of Natural History.

Distribution.—This species is common and widely distributed in the eastern Pacific. Only larval records for EASTROPAC I are given in Figure 22 (Ahlstrom, 1971). *C. pauciradiatus* occurs to the north into the Gulf of California (Fig. 23) where it is rather common. In the central North Pacific it was common off Hawaii and was taken to the west and north of Hawaii (Fig. 18).

Distinguishing Characters.—JUVENILES AND ADULTS. This species can be distinguished

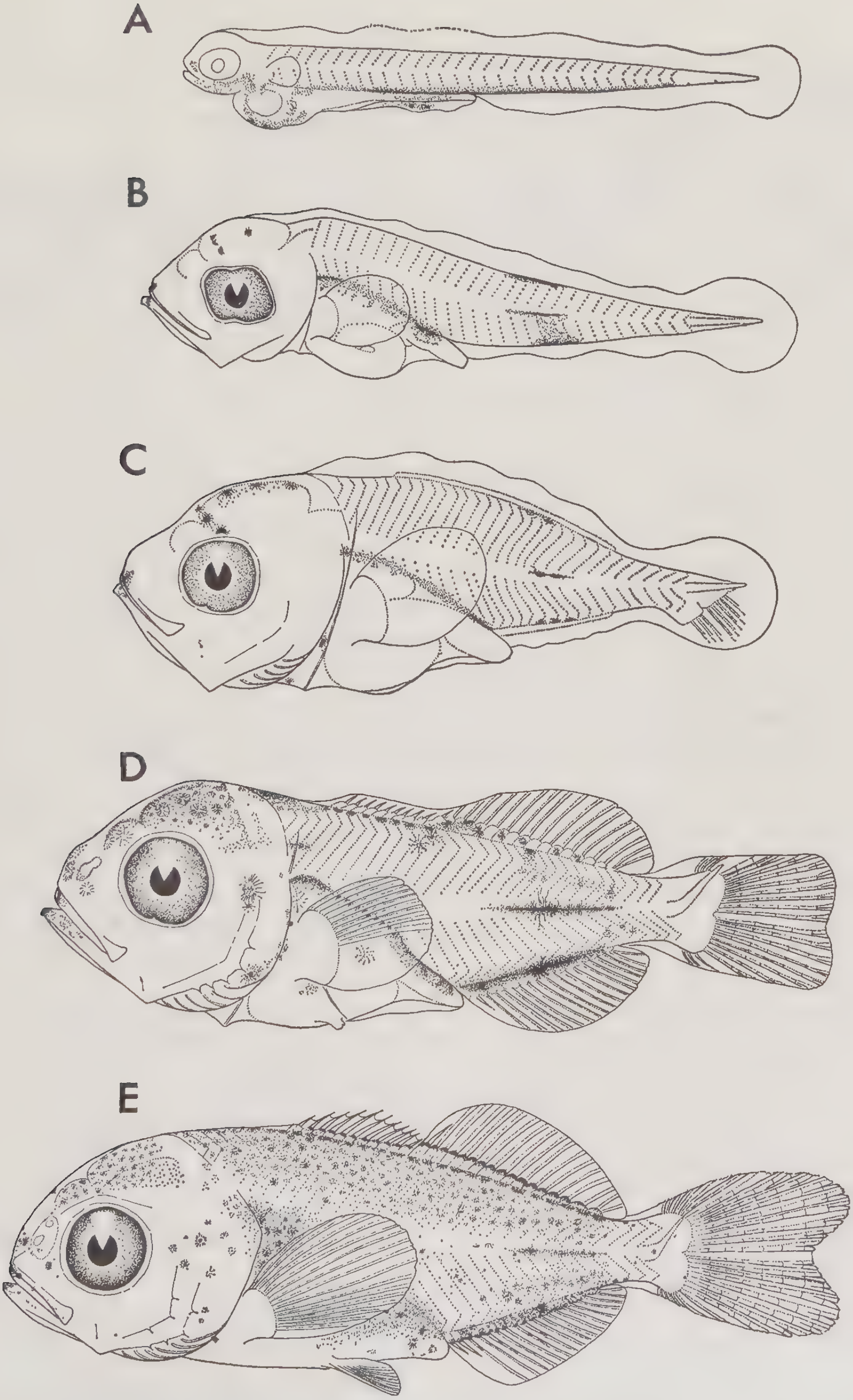


Figure 20. Developmental stages of *Cubiceps pauciradiatus* (Nomeidae). A—2.1-mm preflexion larva; B—3.1-mm preflexion larva; C—3.8-mm early flexion larva; D—5.1-mm postflexion larva; E—8.6-mm postflexion larva.

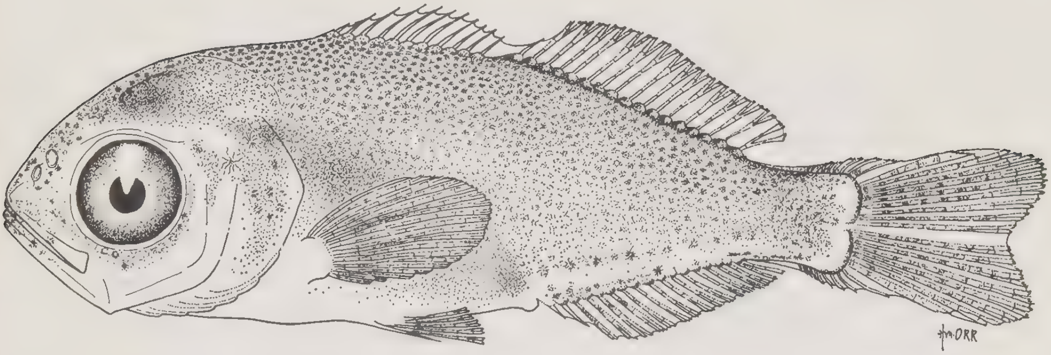


Figure 21. Early juvenile of *Cubiceps pauciradiatus* (Nomeidae), 17.5 mm.

from all other nomeids by the low second dorsal and anal fin ray counts, the bony keel on the breast, the slender body and the broad patch of teeth on the blade of the vomer and glossohyal. Among nomeids with 31 total vertebrae, this is the only species consistently with 13 (rarely 14) precaudal vertebrae. Only *C. capensis* and this species have two anal spines rather than three among *Cubiceps*. Adults attain a length of less than 200 mm (Haedrich, 1967).

LARVAE. Preflexion larvae of *C. pauciradiatus* are most readily distinguished by the pigment pattern, which is discussed under pigmentation. This characteristic pigment consists of opposing dorsal, lateral, and ventral streaks on about myomeres 20 to 23. On postflexion larvae, fin meristics can be used in addition to pigmentation; larvae as small as 5 mm have obtained their full complement of dorsal and anal fin rays.

Meristics.—Vertebrae 13 + 18 = 31 (rarely 13 + 17 = 30 or 14 + 17 = 31). First dorsal X to XII (average 10.9); second dorsal I, 15 to 17 (average I, 16.1); anal II, 14 to 16 (average II, 15.0); principal caudal rays 9 + 8; secondary caudal rays 8 to 10 dorsal + 8 to 10 ventral (average 9.0 + 9.0).

Meristics of 25 specimens from about 9°S to about 23°N and from about 89° to 158°

Table 29. Morphometrics, in mm, of *Cubiceps capensis*, *Cubiceps* sp. A, and *Cubiceps* sp. B (all specimens are juveniles except 8.7-mm postflexion larva)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
Cubiceps capensis									
Step I-32	13.9 SL	8.2	4.3	1.6	1.2	4.2	5.6	8.5	5.4
Cato II-B3119	15.7	9.4	5.2	1.8	1.4	5.4	6.6	9.7	6.2
Cubiceps sp.A									
ETP 11.068	8.7 SL	5.0	3.0	1.1	0.56	3.7	4.1	5.2	3.3
T.C. 51.081	14.0	7.7	4.8	1.9	1.1	5.6	5.8	8.0	5.2
Jord. 60.150	19.5	11.0	6.4	2.3	1.4	7.1	8.0	11.4	7.0
Cubiceps sp.B									
J7210-31.145	12.5 SL	7.0	4.3	1.6	0.9	4.7	5.1	7.1	4.6
Aries 9-H17	17.9	10.0	5.6	2.2	1.2	6.8	7.0	10.4	6.5
Aries 9-A2	18.7	10.4	6.1	2.4	1.3	7.3	7.2	10.7	6.6

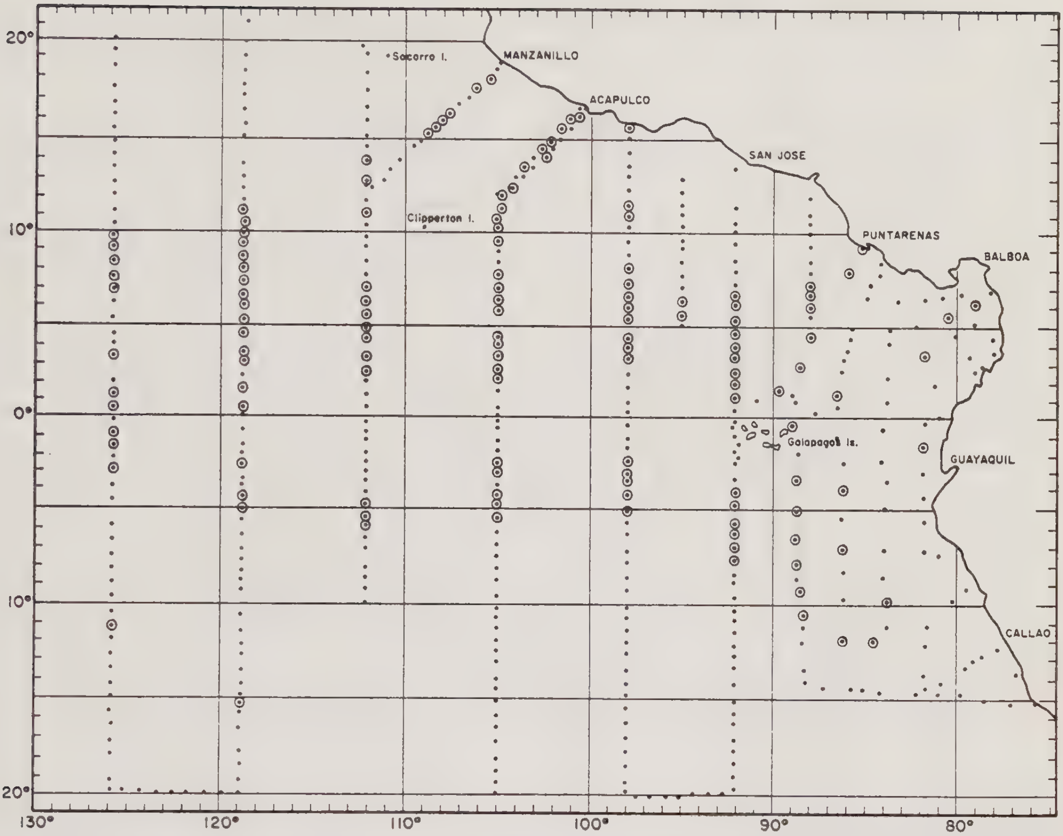


Figure 22. Occurrences of *Cubiceps pauciradiatus* larvae on EASTROPAC I. Records of larvae are indicated by open circles with dot and negative hauls by small dots.

W are given in Table 30. No geographical variation in any count is indicated.

Morphometrics.—Morphometrics of a size series of *C. pauciradiatus* are presented in Table 31. Body proportions are given along with other species of *Cubiceps* in Table 24. See the earlier comparative discussion of *Cubiceps* morphometrics.

Ossification.—The principal caudal rays are first to ossify in *C. pauciradiatus*, with 3 + 3 rays developed on a 3.7-mm specimen (Table 32). The full complement of 9 + 8 principal rays are present by 4.5 mm when secondary caudal rays begin to form. The adult number of 9 + 9 secondary rays is complete in a 12.4-mm specimen. The second dorsal, anal, and pectoral fins begin to develop by 4.5 mm and complete their formation in that respective order by 5.0 mm, 6.2 mm, and 10.0 mm. The first dorsal fin spines begin ossifying by 5.0 mm, and a full count of XI is attained by 6.2 mm. The pelvic fins are the last fins to start development with a count of I, 4 on a 6.2-mm specimen, but they obtain the full array of one spine and five rays before 8.8 mm.

The vertebral bones begin formation early with anterior neural spines ossifying by 3.7 mm. The total number of 31 vertebrae is present by 6.2 mm.

Branchiostegal rays form very early with 0 + 4 rays ossifying on each side in a 3.1-mm specimen and the complete number (2 + 4)

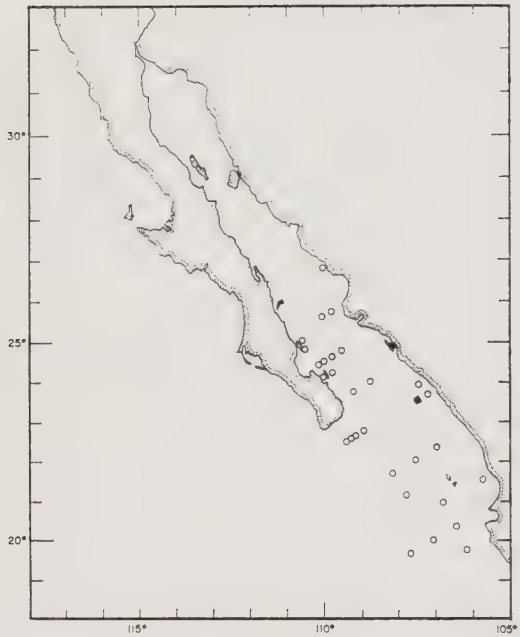


Figure 23. Occurrences of *Cubiceps pauciradiatus* larvae (open circles) and *Nomeus gronovii* (solid square) in the Gulf of California and adjacent areas.

ossifying by 3.7 mm. Gill rakers begin developing on the first arch by 3.7 mm but full counts are still not obtained in a 22.2-mm specimen.

Four to five weak spines form on the margin of the preopercle at about 5.0 mm and subsequently several appear on the preopercular ridge at about 8.5 mm. These preopercular spines are resorbed beginning at about 11.2 mm and are never a conspicuous feature during the larval period of development.

Teeth in larvae and early juveniles are small, uniserial, and gradual in development. Premaxillary and dentary teeth first appear by 6.2 mm and slowly increase in number (Table 32). Minute lateral teeth develop at right angles to the regular teeth on the lower jaw of early juveniles, but these are gone by 22.2 mm. The regular teeth are small, broad-based but sharply pointed, and sometimes slightly recurved. No teeth on the palatines or blade of the vomer are evident at 22.2 mm. Development of glossohyal teeth in early juveniles is discussed in an earlier comparative section on dentition of the stromateoid fishes.

Lateral line scales are developed by 12.4 mm, then gradually spread over other parts of the body. Specimens at this size and larger can be classed as juveniles, inasmuch as all fins are complete and scale formation has begun.

Pigmentation.—In newly hatched larvae of *C. pauciradiatus*, the pigment is distributed along the back with a patch of pigment on the snout much like advanced embryos (as shown in Fig. 2). The pigment migrates ventrally, extending in a continuous line above the gut and along the ventral margin of the tail just short of the notochord tip. At this stage, there is pigment under the head and on the ventral margin of the gut, but the eyes are not yet pigmented; larvae are 1.5 to 2.2 mm long (Fig. 20A). Pigment on the tail soon concentrates into a conspicuous ventral patch beginning about three myomeres behind the anus and extending over three to seven myomeres. A series of two to five small ventral pigment spots persist on the tail just forward of the notochord tip. At this stage, the eyes are pigmented, the mouth is well formed and the body is beginning to deepen; the larvae are about 2.0 mm long. Early preflexion larvae between 2.0 and 2.5 mm develop a lateral line dash of pigment above the ventral streak, and by about 3.0 mm, form an opposing dorsal patch (Fig. 20B). Meanwhile, the pigment under the gut has coalesced into one or two spots posterior to the cleithrum, and these disappear before flexion, but a spot appears forward of the cleithrum on the ventral margin (Figs. 20C and 29K). Some pigment develops on the top of the head and on both jaws prior to flexion. Unlike *C. caeruleus*, there is no pigment streak developed through the midline of the eye on larvae of *C. pauciradiatus*.

Pigmentation during flexion does not

Table 30. Meristics of 25 juveniles and adults of *Cubiceps pauciradiatus* selected from over its distributional range in the eastern Pacific, including off Hawaii (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
MV 68-I-4	22°42.7'N	109°54'W	I.9.69	69.9	13+18=31	XI	I,16	II,15	9-17-9
T.C. 32.005	21°22'N	158°13'W	VII.13.67	84.0	13+18=31	XI	I,17	II,16	9-17-9
T.C. 32.023	21°00'N	158°30'W	VII.22.67	96.0	13+18=31	XI	I,17	II,16	9-17-9
Defiance 68(1)-6	19°36'N	111°07'W	VIII.19.68	115.0	13+18=31	XI	I,16	II,15	8-17-8
ETP 50.134	17°11'N	106°44'W	XI.6.67	55.3	13+18=31	XI	I,16	II,15	9-17-9
Scot Exped. #81	14°47'N	94°21'W	V.29.58	55.0	13+18=31	XI	I,16	II,15	10-17-10
Jord. 57.013	13°27'N	119°01'W	XI.9.70	110.0	13+18=31	XI	I,16	II,15	9-17-10
Jord. 57.012	13°16'N	119°23'W	XI.9.70	117.0	13+18=31	XI	I,17	II,15	9-17-9
TO 59(1)-28	12°41'N	91°35'W	II.8.59	30.5	13+18=31	XI	I,16	II,15	9-17-9
Jord. 77.166	11°31'N	121°18'W	II.8.73	23.7	13+17=30	XI	I,16	II,14	8-17-8
Jord. 57.024	10°47.5'N	119°30'W	XI.11.70	93.0	13+18=31	XI	I,16	II,15	10-17-10
Jord. 57.052	10°05'N	117°42'W	XI.16.70	11.6	13+18=31	XI	I,16	II,15	8-17-8
Jord. 57.041	10°00'N	118°20'W	XI.13.70	87.0	13+18=31	XI	I,17	II,15	9-17-9
TO 58(2)-A/B	09°48.5'N	89°14.5'W	XI.22.58	28.0	13+18=31	X	I,16	II,15	9-17-9
Jord. 57.113	07°14.6'N	119°24'W	XII.7.70	25.0	13+18=31	XI	I,16	II,15	10-17-10
ETP 13.340	05°37'N	94°56'W	III.20.67	15.6	13+18=31	X	I,16	II,15	9-17-9
TO 58(1)-56	05°31.5'N	86°43'W	V.16.58	43.6	13+18=31	XI	I,16	II,14	9-17-9
Jord. 65.025	04°22'N	97°58'W	VIII.24.71	20.5	13+18=31	XI	I,17	II,15	9-17-9
T.C. 51.087	01°17'N	120°06'W	XI.20.70	122.0	13+18=31	XI	I,17	II,16	9-17-8
Jord. 65.214	00°30'S	97°13'W	IX.28.71	36.0	13+18=31	XI	I,16	II,14	9-17-9
T.C. 51.056	03°12'S	119°26'W	XI.10.70	124.0	13+18=31	XI	I,16	II,16	9-17-9
T.C. 51.071	03°12'S	121°27'W	XI.14.70	113.0	13+18=31	XI	I,15	II,15	9-17-9
T.C. 51.048	04°02'S	118°48'W	XI.8.70	107.0	13+18=31	XI	I,15	II,14	9-17-9
ETP 13.071	04°16'S	92°05'W	II.16.67	18.3	13+18=31	XI	I,16	II,14	9-17-9
Jord. 65.108	09°00'S	98°00'W	IX.3.71	107.0	14+17=31	XI	I,17	II,15	9-17-9

change significantly from that of late preflexion except for increased pigment on the head (Fig. 20C).

Following flexion, however, pigment formation is augmented. By 5.1 mm (Fig. 20D), the upper head region becomes densely pigmented and scattered melanophores develop on the snout and opercle. Accentuated pigment forms on the shoulder and along the bases of the dorsal and anal fins, with melanophores also appearing between the dorsal, lateral, and ventral pigment streaks.

By 8.6 mm (Fig. 20E), the upper portion of the abdomen and the dorsal half of the body, except the caudal peduncle region, become uniformly pigmented. Pigment gradually spreads over the caudal peduncle area in early juveniles, and by 17.5 mm (Fig. 21), *C. pauciradiatus* is covered with pigment although still sparse ventrally.

Discussion.—In the original description of *C. carinatus*, Nichols and Murphy (1944) noted that the combination of long pectorals and rather short dorsal and anal fins was shared by several other species. However, they considered the keeled breast and large deciduous scales to be unique to their species, which they placed in a new subgenus, *Mandelichthys*. Haedrich (1965), in his description of *C. athenae* Haedrich, noted that the keeled breast, large deciduous scales, two anal spines, and low ray counts in the dorsal and anal fins were unifying characters for five nominal species in the subgenus *Mandelichthys*: *C. pauciradiatus*, *C. longimanus* Fowler (1934), *C. nesiotes* Fowler (1938), *C. carinatus* and *C. athenae*. Haedrich (1965, 1967) placed *C. nesiotes* Fowler as a probable synonym of *C. pauciradiatus*. Haedrich (1972) indicated that *C. longimanus* Fowler was also probably synonymous with *C. pauciradiatus* and suggested that *C. athenae* may be an Atlantic synonym of *C. pauciradiatus*.

Table 31. Morphometrics, in mm, of larvae and juveniles of *Cubiceps pauciradiatus* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 60.062	2.1 NL	1.1	0.44	0.14	0.11	0.35	-	-	-
ETP 60.060	2.5	1.3	0.46	0.21	0.15	0.46	-	-	-
ETP 13.048	3.1	1.8	0.82	0.30	0.28	1.0	-	-	-
ETP 60.195	3.8	2.2	1.1	0.46	0.42	1.2	base	2.2	-
	3.7	2.3	1.3	0.44	0.34	1.3	1.6	2.3	-
ETP 75.198	4.0	2.4	1.3	0.42	0.32	1.4	1.6	2.4	-
ETP 60.195	4.3	2.5	1.4	0.46	0.38	1.6	1.7	2.5	-
H5612-170.G.20	4.4 SL	2.8	1.5	0.54	0.40	1.5	1.9	2.8	1.8
ETP 75.198	5.0	3.2	1.8	0.59	0.48	1.8	2.3	3.4	2.3
ETP 75.048	6.3	4.0	2.2	0.76	0.55	2.3	2.6	3.9	2.6
ETP 45.028	7.4	4.8	2.6	0.97	0.71	2.8	3.3	5.3	3.2
H5612-170.G.30	8.6	5.2	2.8	0.99	0.71	3.0	3.3	5.4	3.5
ETP 12.246	9.4	5.9	3.1	1.1	0.84	3.2	3.8	6.0	4.1
H5612-170.G.20	10.0	6.2	3.4	1.2	0.80	3.3	4.0	6.3	4.2
ETP 30.248	11.2	7.2	4.0	1.3	0.83	4.0	4.5	7.3	4.8
"	12.4*	7.8	4.4	1.5	1.1	4.4	5.2	8.4	5.4
ETP 45.325	13.5*	8.4	4.6	1.7	1.0	4.5	5.5	9.0	5.5
ETP 30.248	14.2*	8.8	4.8	1.7	0.92	4.7	5.7	9.2	6.0
ETP 11.213	15.0*	9.7	5.2	1.7	1.1	5.1	6.0	10.0	6.5
ETP 20.195	16.0*	10.0	5.2	1.7	1.2	5.2	6.2	10.2	6.7
Hawaii 70-9-23	17.5*	11.0	6.0	2.0	1.3	5.7	6.5	10.9	7.0
ETP 45.028	22.2*	13.0	6.8	2.5	1.3	6.6	7.8	13.4	8.3
Hawaii 71-6-2	27.5*	17.2	8.4	3.1	2.1	7.7	10.2	17.4	11.5

* Juvenile

Haedrich (1965, 1972) distinguished *C. athenae* from *C. pauciradiatus* on the basis of a precaudal vertebral count of 13 rather than 14. We have observed that small specimens of *C. pauciradiatus* from the Pacific, Indian, and Atlantic oceans almost always have 13 + 18 = 31 vertebrae. In radiographs of larger specimens, however, the precaudal vertebrae can be read as 14 or even 15, inasmuch as the haemal spines on vertebrae 14 and 15 in larger specimens are markedly bent posteriorward and are less conspicuous than the pleural ribs that also are developed on these vertebrae (Fig. 1). Since the vertebral counts are in fact the same, *C. athenae* should be regarded as a synonym of *C. pauciradiatus.*

The dorsal and anal fin ray counts of *C. carinatus* given by Nichols and Murphy (1944) are lower than that of *C. pauciradiatus.* Radiographs of the type and paratype show higher counts. The type of *C. carinatus*, 103 mm SL, has 13 + 18 = 31 vertebrae; dorsal XI, I, 15; anal II, 15; caudal 9-17-9. The paratype, 91 mm SL, has 13 + 18 = 31 vertebrae; dorsal XI, I, 15; anal II, 15; and caudal 7-17-7. The counts fall within the range of *C. pauciradiatus.* The arrangement of anal pterygiophores in relation to haemal spines is precisely the same as in *C. pauciradiatus.* Further, larvae from the Atlantic, Indian, and Pacific oceans do not indicate more than one species. We therefore consider *C. carinatus* a junior synonym of the cosmopolitan *C. pauciradiatus.*

Cubiceps
sp. A
Figure 24

Literature.—To date, secondary caudal rays have not been given in the literature for nomeids. For that reason, we are not able to assign this species to any described for the genus *Cubiceps.*

Material.—We examined three specimens from the eastern tropical Pacific, 8.7, 14.0 and 19.5 mm (Table 28), and two specimens, 40.5 mm and 43.7 mm, from the China Sea, taken on the Scripps Naga expedition. The latter two specimens are not

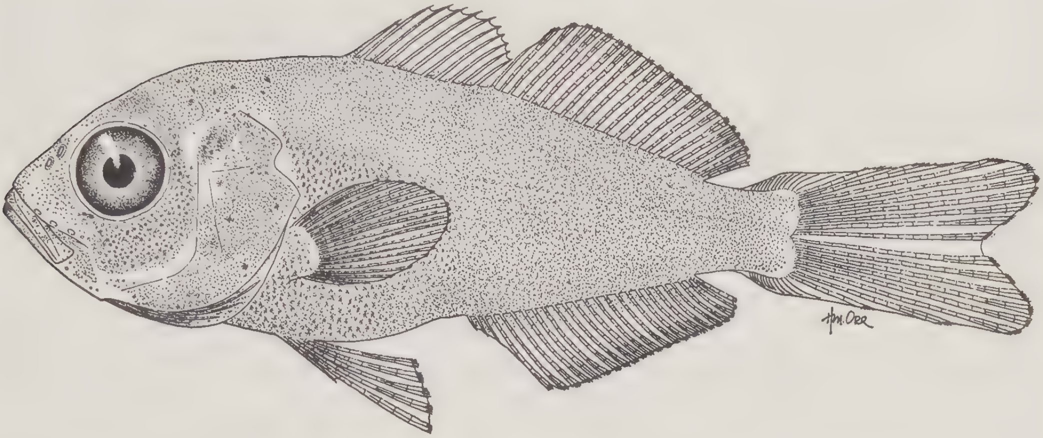


Figure 24. Early juvenile of *Cubiceps* sp. A (Nomeidae), 19.5 mm.

included in the meristic or morphometric tables (Tables 28 and 29).

The radiograph of a 429-mm specimen in the South African Museum shows characters of *Cubiceps* sp. A. The secondary caudal ray count is somewhat lower with 11 + 10 rays. The specimen has 12 + 19 = 31 vertebrae, a dorsal count of XI, I, 22; anal fin count of III, 22, and a predorsal pterygiophore pattern of 0/0/0 + 2/. The pattern of interdigitation of anal pterygiophores with haemal spines fits the pattern given for *C.* sp. A (Table 3).

Table 32. Meristics of cleared and stained larvae and juveniles of *Cubiceps pauciradiatus* (specimens between dashed lines are undergoing notochord flexion)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Brancniostegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 13.048	3.1 NL	-	-	-	-	-	-	-	0+4	-	-	-
ETP 75.198	3.8	-	-	-	-	-	-	-	2+4	-	-	-
ETP 13.191	3.7	-	-	-	-	-	0-3+3-0	9+ 0= 9†	1+4	0+1+0	-	-
ETP 60.195	3.7	-	-	-	-	-	0-4+4-0	9+ 0= 9†	2+4	0+1+0	-	-
"	3.8	-	-	-	-	-	0-5+4-0	-	2+4	-	-	-
ETP 13.243	4.5 SL	-	I,13	I,11	7	-	0-9+8-1	13+10=23†	2+4	0+1+7	-	-
ETP 75.198	5.0	IX	I,15	I,16	10	-	0-9+8-1	13+14=27†	2+4	0+1+7	-	-
ETP 60.195	6.2	XI	I,16	II,15	15	I,4	4-9+8-4	13+18=31	2+4	0+1+10	1	1
ETP 75.048	6.3	XI	I,16	II,15	14	I,3	4-9+8-4	13+18=31	2+4	0+1+10	0	1
ETP 45.028	7.4	XI	I,14	II,15	16	I,4	5-9+8-5	13+18=31	2+4	0+1+10	0	2
ETP 13.048	8.8	XI	I,16	II,16	16	I,5	7-9+8-7	13+18=31	2+4	2+1+10	3	3
H5612-170.G.20	10.0	XI	I,16	II,14	17	I,5	7-9+8-7	13+18=31	2+4	4+1+11	6	3
ETP 13.048	11.2	XI	I,16	II,15	17	I,5	6-9+8-7	13+18=31	2+4	4+1+11	5	8
ETP 30.248	12.4*	XI	I,16	II,15	17	I,5	9-9+8-9	13+18=31	2+4	6+1+13	9	9
"	14.2*	XI	I,15	II,15	19	I,5	9-9+8-9	13+18=31	2+4	6+1+12	10	9
ETP 11.213	15.0*	XI	I,16	II,15	19	I,5	9-9+8-9	13+18=31	2+4	7+1+13	13	11
ETP 20.195	16.0*	XI	I,16	II,15	19	I,5	8-9+8-9	13+18=31	2+4	6+1+13	16	13
Jord. 57.030	18.4*	XI	I,17	II,16	19	I,5	9-9+8-9	13+18=31	2+4	7+1+13	10	14
ETP 45.028	22.2*	XI	I,16	II,15	19	I,5	10-9+8-9	13+18=31	2+4	7+1+13	15	12
Jord. 57.047	52.0*	XII	I,16	II,15	18	I,5	9-9+8-9	13+18=31	2+4	8+1+15	24	29

* Juvenile

† Vertebrae not completely developed

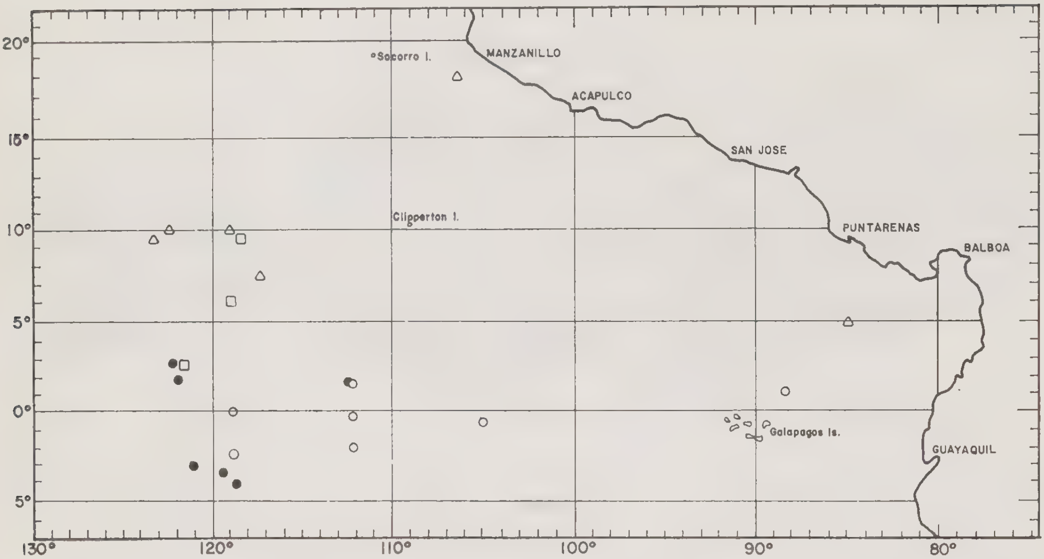


Figure 25. Occurrences of larvae and juveniles of *Cubiceps* sp. A, *Nomeus gronovii*, and *Psenes pellucidus* in the eastern tropical Pacific. Open squares indicate larvae and juveniles of *Cubiceps* sp. A and open triangles indicate larvae and juveniles of *Nomeus*. Larvae of *P. pellucidus* indicated by open circles, juveniles by closed circles.

Distribution.—This species appears to have a tropical distribution (Fig. 25).

Distinguishing Characters.—*Cubiceps* sp. A is very similar to *C. caeruleus* and *C.* sp. B. It may be separated from *C. caeruleus* by its higher number of secondary caudal rays (12 + 12 compared to 7–10 + 7–10, average 8.7 in *C. caeruleus*), its different arrangement of anal fin pterygiophores in relation to haemal spines (Table 3) and its denser pigmentation over the entire body (Fig. 24). *C.* sp. A may be separated from species B by its higher number of second dorsal and anal fin rays (Table 28) and its sparsely pigmented fins (compare Figs. 24 and 26B). As noted in the following pigmentation section, larvae of *C.* sp. A become heavily pigmented at smaller sizes than other *Cubiceps*; the contrast in this character between *C.* sp. A and *C.* sp. B is particularly marked.

Meristics.—Vertebrae 12 + 19 = 31; first dorsal XI; second dorsal I, 22 or 23; anal III, 21 or 22; principal caudal rays 9 + 8; secondary caudal rays 12 dorsal + 12 ventral; pectoral fin rays, 20 or 21 (Tables 1 and 28).

Morphometrics.—Morphometrics for *C.* sp. A are presented in Table 29 and body proportions in Table 24. The body shape of *C.* sp. A resembles *C. caeruleus* and especially *C.* sp. B more than *C. capensis* or *C. pauciradiatus*.

Ossification.—Ossification data are not available due to the limited amount of material.

Pigmentation.—The 8.7-mm specimen of *C.* sp. A has the head and body completely covered with dense pigmentation except along the bases of the dorsal, anal, and caudal fins. Of all the fins, only the pelvics are pigmented. This species becomes heavily pigmented at a smaller size than any other *Cubiceps* species examined for the present work.

The two larger specimens, 14.0 and 19.5

mm (see Fig. 24 for 19.5-mm specimen) are similarly heavily pigmented except over the posterior margins of the hypural bones. The pelvic fins are pigmented adjacent to the body; the dorsal and anal fins have a sprinkling of pigment immediately adjacent to the body but are otherwise unpigmented; the base of the pectoral fin is pigmented but not the blade; the caudal fin is unpigmented.

Although the body is strongly pigmented on *C.* sp. A, the fins other than the pelvics are virtually without pigment. This contrasts with the conspicuously pigmented fins on *C.* sp. B.

Cubiceps
sp. B
Figure 26

Literature.—As with *C.* sp. A, *C.* sp. B cannot be assigned to any described species of *Cubiceps* since secondary caudal rays are not discussed in the literature. However, we strongly suspect that a large (586 mm) specimen of a nomeid taken off Portuguese Bend, California, and reported in the literature as *C. gracilis* (Fitch and Lavenberg, 1968) is the adult of species B. This specimen has a similarly high secondary caudal ray count of 12 + 12, 12 + 19 = 31 vertebrae, a dorsal fin count of XI, I, 21 and an anal fin count of III, 21. The specimen appears to lack teeth on the tongue and on the blade of the vomer.

Material.—Three specimens, 12.5 mm, 17.9 mm, and 18.7 mm, were available from the central water mass of the eastern North Pacific (Table 28).

Distribution.—This species appears to be a temperate water species in the North Pacific (Fig. 18).

Distinguishing Characters.—*C.* sp. B is closely allied to species *C.* sp. A and *C. caeruleus.* Species B can be distinguished from species A by its lower second dorsal and anal ray counts (Table 28) and different pigment pattern, and from *C. caeruleus* by its higher number of secondary caudal rays and its different pattern of haemal spine interdigitation with anal fin pterygiophores (Table 3).

Meristics.—Vertebrae 12 + 19 = 31; first dorsal XI; second dorsal I, 19 or 20; anal III, 20; principal caudal rays 9 + 8; secondary caudal rays 11 or 12 dorsal + 12 ventral; pectoral fin rays, 22 (Tables 1 and 28).

Morphometrics.—Morphometrics for *C.* sp. B are given in Table 29 and body proportions in Table 24. Species A and sp. B are strikingly similar in body shape and body proportions. The only body proportion showing any difference in the two forms was snout to origin of dorsal fin: 41 to 47% of SL in sp. A and 38 to 41% of SL in sp. B.

Ossification.—No data on the sequence of ossification are available with only three specimens in the collection, all of which have complete fins.

Pigmentation.—The smallest of the three specimens of *C.* sp. B in our collection, 12.5 mm, has most of its tail portion of the body unpigmented (Fig. 26A). The pigment pattern at this stage is reminiscent of that found on smaller sized (ca. 6.2 mm) *C. caeruleus*, except for the line of melanophores along the bases of the dorsal and anal fins, which is reminiscent of pigment augmentation in *C. pauciradiatus.*

The method in which pigment fills in over the tail portion of the body is not known, as the two larger specimens of 17.9 and 18.7 mm (Fig. 26B) are entirely covered with pigment with sparse pigment areas below the head and abdomen. The first dorsal, pelvic, and caudal fins are heavily pigmented but only the anterior portions of the second dorsal and anal fins and the base of the pectorals are sprinkled with pigment.

Genus *Nomeus*

It is now generally agreed that there is only one widely distributed species in this genus. No differences were observed between specimens from the Atlantic and Pacific oceans.

Nomeus gronovii
(Gmelin, 1788)
Figures 27 and 28

Literature.—Eigenmann (1894) reported a specimen taken in a tidepool on the Gulf of Panama, a

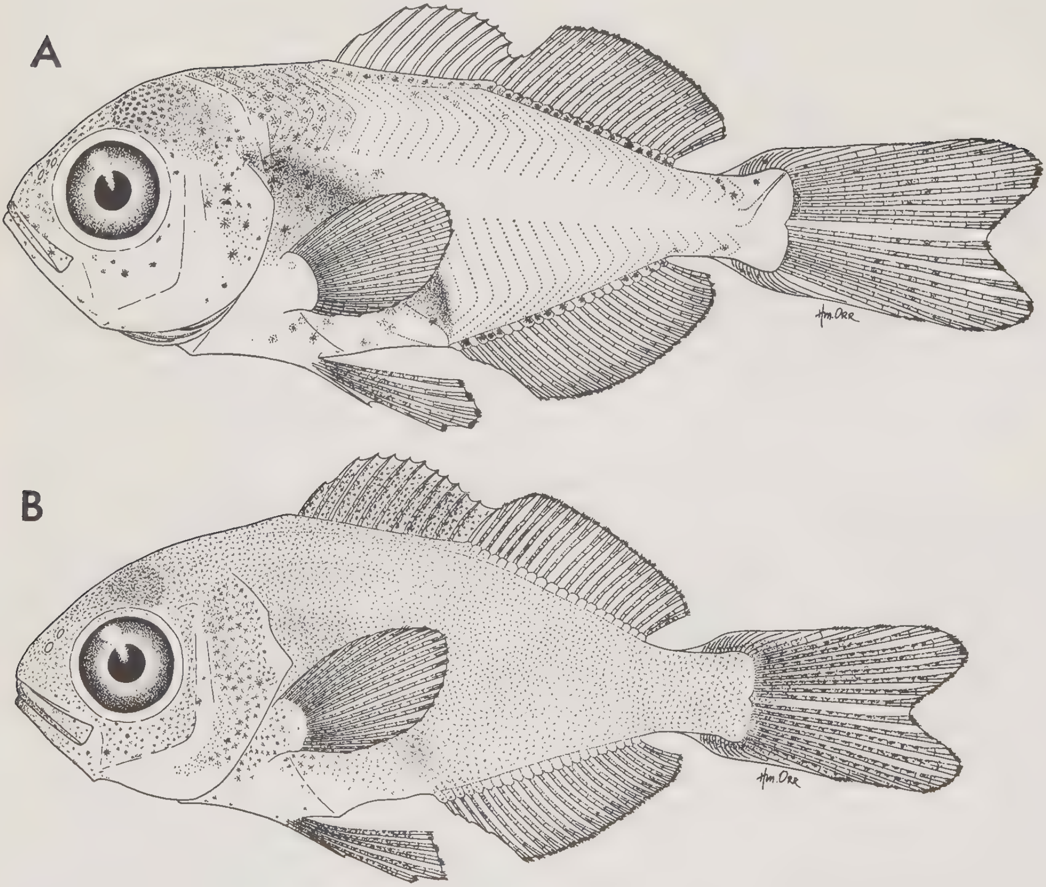


Figure 26. Early juveniles of *Cubiceps* sp. B (Nomeidae). A—12.5 mm; B—18.7 mm.

most unusual collection locality. Fowler (1928) reported this species from the Hawaiian Islands. Fitch (1953) reported on a specimen taken under a jellyfish from Gordo Point, Baja California. Gooding and Magnuson (1967) observed a specimen at the equator south of Hawaii under a drifting raft.

Material.—Seven specimens of postflexion larvae and juveniles from the eastern tropical Pacific and a moderate number of juveniles from the western North Atlantic were studied.

Distribution.—This species was taken from widely scattered localities in the eastern Pacific. All of the collections are north of 5°N and most are well offshore (Fig. 25). One specimen was taken at the mouth of the Gulf of California (Fig. 23).

Distinguishing Characters.—JUVENILES. *Nomeus* is distinguished by the conspicuous banded pigment pattern on its body and by the large, heavily pigmented pelvic fins. Like some *Psenes pellucidus*, it has 41 vertebrae but differs in having only two anal fin spines, not three.

LARVAE. Postflexion larvae also may be distinguished by the high myomere count, dorsal and anal fin meristics, and pigmentation. Larvae of 7.0 to 8.0 mm may have pigment patches similar to comparable sized *P. cyanophrys*, but *Nomeus* is separated by its higher meristics (especially vertebrae) and more streamlined body. Preflexion larvae are lacking.

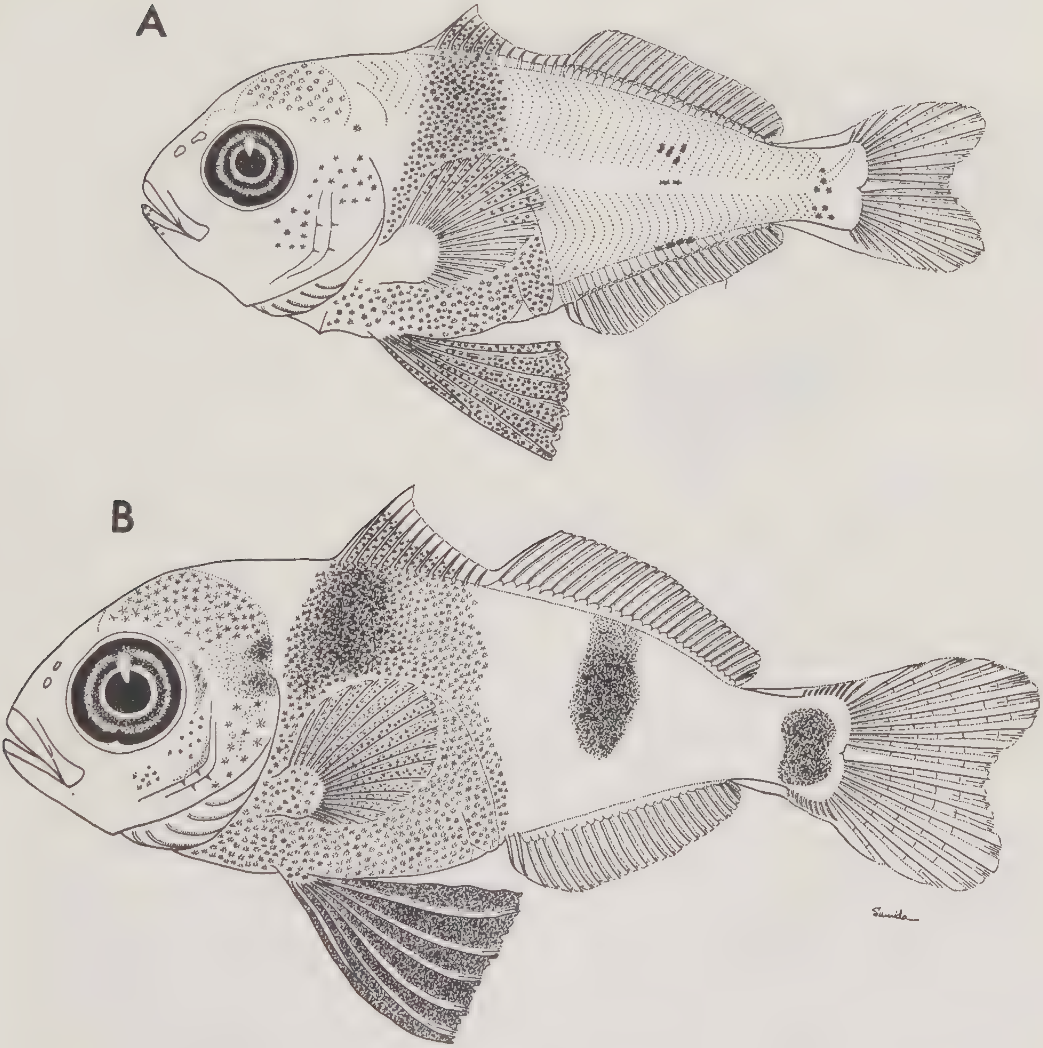


Figure 27. Developmental stages of *Nomeus gronovii* (Nomeidae). A—7.3-mm postflexion larva; B—9.2-mm early juvenile.

Meristics.—Vertebrae 14 + 27 = 41; first dorsal XI or XII (average 11.6); second dorsal 25 to 27 (average 25.9); anal II, 24 to 26 (average II, 25.1); principal caudal rays 9 + 8; secondary caudal rays 8 or 9 dorsal + 8 or 9 ventral (average 8.8 + 8.6) (Table 1).

Morphometrics.—Seven postflexion larvae and early juveniles of *N. gronovii*, 7.3 to 27.5 mm in length, were available for morphometric measurements (Table 33). In some body features, *Nomeus* is similar to *Psenes*, in others, to *Cubiceps*. The snout to anus distance of 56 to 59% of SL (Table 10) is longer than for *Psenes*, but within the range for *C. caeruleus*. The head length of 30 to 34% of SL is about average for nomeids as are the eye diameter of 38 to 44% of HL, and the snout length of 19 to

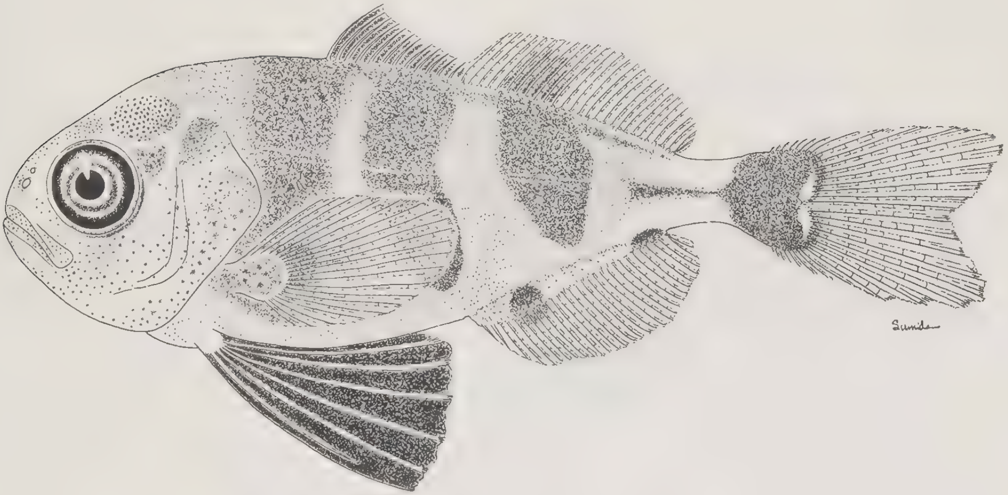


Figure 28. Early juvenile of *Nomeus gronovii* (Nomeidae), 22.7 mm.

25% of HL. The body depth at base of pectoral fins of 37 to 41% of SL is less than for any species of *Psenes* except *P. sio*, but within the range of several species of *Cubiceps*. The distance from the snout to the anal fin origin of 57 to 61% of body length is longer than for most *Psenes*, but within the range of several species of *Cubiceps*. However, the forward position of the pelvic fin origin of 26 to 34% of SL is closer to *Psenes* than to *Cubiceps*.

Ossification.—Data on the sequence of ossification are not available since the smallest specimen examined, 7.3 mm SL, has most of its fins developed (Fig. 27A). Meristics for the seven specimens examined are presented in Table 34.

Pigmentation.—Larval and juvenile *Nomeus* have large and heavily pigmented pelvic fins and prominent pigment bands on the body. Postflexion larvae have pigment most developed on the body above the pelvic fins. On the 7.3-mm specimen the tail pigment is very similar to *Psenes* larvae; there is opposing lateral and ventral pigment, and pigment over the hypural bones (Fig. 27A). Pigment is very heavy over the abdomen and extends dorsally in a dark band up to the anterior six spines of the first dorsal fin. However, the space between the pigmented head and

Table 33. Morphometrics, in mm, of postflexion larvae and juveniles of *Nomeus gronovii*

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
S.B. 162	7.3 SL	4.2	2.4	0.92	0.58	2.8	2.9	4.4	2.5
ETP 45.358	7.5	4.2	2.5	1.1	.52	3.1	3.0	4.3	2.3
Jord. 57.035	8.9	5.0	2.9	1.2	.56	3.4	3.5	5.2	2.7
Jord. 77.119	9.2*	5.4	3.1	1.2	.64	3.5	3.6	5.6	2.8
Jord. 77.155	9.9*	5.6	3.3	1.4	.84	3.7	3.8	5.8	2.7
J7205-157G130	11.9*	6.8	3.6	1.6	.72	4.7	4.6	7.0	3.1
Jord. 77.144	27.5*	14.4	8.2	2.7	1.7	9.2	9.7	15.2	6.0

* Juvenile

Table 34. Meristics of postflexion larvae and early juveniles of *Nomeus gronovii* (Note: only 9.2-mm specimen cleared and stained; vertebral counts of 7.3-mm and 7.5-mm specimens are myomere counts; counts for remaining specimens taken from radiograph)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Brancniostegal rays	Gill rakers (right)	Teetn (left)	
											Prem.	Dent.
S.B. 162	7.3 SL	XII	25	II,25	17	I,5	3-9+8-3	14+27=41	2+4	3+1+10	2	1
ETP 45.358	7.5	XI	ca 27	ca I,25	16	I,5	7-9+8-7	14+27=41	2+4	3+1+11	3	2
Jord. 57.035	8.9	XI	25	I,26	18	I,5	9-9+8-9	14+27=41	2+4	3+1+10	4	ca 2
Jord. 77.119	9.2*	XII	26	II,25	19	I,5	9-9+8-9	14+27=41	2+4	3+1+11	8	4
Jord. 77.155	9.9*	XI	27	I,26	19	I,5	9-9+8-9	14+27=41	2+4	3+1+11	7	4
J7205-157G130	11.9*	XII	26	II,25	20	I,5	8-9+8-8	14+27=41	2+4	3+1+12	ca 8	5
Jord. 77.144	27.5*	XII	25	II,24	ca 19	I,5	9-9+8-8	14+27=41	2+4	6+1+14	ca 21	ca 11

* Juvenile

the origin of the first dorsal fin remains unpigmented, even on the 9.2-mm specimen. On this specimen the lateral and ventral pigment on the tail have become a large patch under the second dorsal fin (Fig. 27B). The pigment on the hypural bones has become a prominent patch. The pigment on the head has intensified.

The 22.7-mm juvenile has four conspicuous bands of pigment on the body (Fig. 28). There are two bands of pigment under the first dorsal fin, whereas in *Psenes* there is only one band in this region. *Nomeus* has only one band of pigment under the second dorsal, whereas at this size *Psenes* has two or three bands under this fin. The hypural pigment is well developed in both genera. At this size, the pigment under the abdomen has been lost, but the nape is now pigmented. The first dorsal fin as well as the pelvic fins are heavily pigmented. The single pigment patch under the second dorsal fin extends out onto the fin. There are two small ventral pigment patches that extend onto the anal fin. The anal fin is otherwise unpigmented as is the caudal fin.

Genus *Psenes*

Five species of *Psenes* have been collected from the eastern Pacific. Four of the species also occur in the North Atlantic (Haedrich, 1972), and it has been our good fortune to be able to examine larvae and juveniles of three of these: *P. cyanophrys*, *P. maculatus*, and *P. pellucidus*. *P. arafurensis* also is known from the tropical Atlantic and Indian oceans. Only *P. sio*, the common species in the eastern tropical Pacific and Gulf of California, appears to have a distribution limited to the eastern Pacific. We have examined only larvae and juveniles of *Psenes*; adults were not available. The largest juveniles examined of the five species of *Psenes* were as follows: *P. maculatus*, 32.1 mm; *P. sio*, 65.0 mm; *P. cyanophrys*, 80.0 mm; *P. pellucidus*, 95.0 mm; and *P. arafurensis*, 117.0 mm.

Postflexion larvae and early juveniles of *Psenes* usually can be separated from those of *Cubiceps* on the basis of meristics alone; however, separation is more secure when based on a combination of meristics, pigment patterns, morphometrics, and the sequence in which fins form.

Among the five species of *Psenes* from the eastern Pacific, *P. arafurensis* and *P. cyanophrys* have 31 vertebrae, *P. maculatus* has 34 or 35, *P. sio* 36 to 38 and *P. pellucidus* 40 to 42 vertebrae. All five species of *Cubiceps*, however, have only 31 vertebrae. What meristics distinguish among the nomeids with 31 vertebrae?

Cubiceps pauciradiatus averages five less second dorsal and anal fin rays than any eastern Pacific *Psenes*. The two *Cubiceps* designated *C.* sp. A and *C.* sp. B can be separated on the basis of secondary caudal ray counts, as these average approximately four more rays than for the two species of *Psenes* with 31 vertebrae. *C. capensis*, the species of *Cubiceps* with the highest dorsal and anal fin counts, overlaps these counts with *P. cyanophrys*. However, *C. capensis* has one more first dorsal spine (XI vs. X), one less anal spine (II vs. III), and three less anal rays (22.2 vs. 25.2) than *P. cyanophrys*. *C. caeruleus* and *P. arafurensis* have almost identical average dorsal counts, XI, I, 21.2 vs. XI, I, 21.1 but differ in average anal counts (III, 20.6 vs. III, 22.1). *P. arafurensis* is deeper-bodied than *C. caeruleus* and differently pigmented, hence readily separable on pigment and morphometric characters.

The presence of pelvic fins on preflexion larvae of *Psenes*, 3.0 mm and larger, and their absence on preflexion larvae of *Cubiceps* distinguishes between these two genera.

Differences among pigment patterns in larvae and early juveniles of *Psenes* and *Cubiceps* are summarized in a later section under comparative pigmentation. Early juveniles of *Cubiceps* become rather uniformly pigmented over the body whereas early juveniles of *Psenes* have their pigment clustered in bands and patches.

One of the characters used by Haedrich and Horn (1972) to distinguish between *Psenes* and *Cubiceps* is the origin of the first dorsal fin. The origin is before or directly over the insertion of the pectoral fins in *Psenes*, whereas it is over (in small specimens) or behind the base of the pectoral fins in *Cubiceps*. A similar relation usually is present in larvae and early juveniles of these genera.

Comparative Morphometrics

The morphometrics of *Psenes* are shown in Table 35. There are various developmental characters shared in common by all species of *Psenes*. Early preflexion larvae are smaller-headed and much more slender-bodied than late preflexion larvae and subsequent stages. All species of *Psenes* acquire pelvic fins very early, usually by 3.0 mm NL, undergo flexion at fairly small sizes, i.e., 3.8 to 5.9 mm, and complete larval development between 10 to 15 mm. There is no sharp demarcation between the larval and juvenile stages.

In the sections that follow, emphasis will be placed on postflexion larvae and early juveniles.

Head Length.—Head length ranges between 22 to 29% of NL on preflexion larvae of *Psenes*, between 29 to 36% of NL on flexion specimens, and between 27 to 39% of SL on postflexion specimens. The head is proportionately shorter on the two species with higher vertebral counts, *P. pellucidus* and *P. sio*, although the differences among species is quite moderate. Head length averages 30% of SL in *P. pellucidus*, 32% of SL in *P. sio*, and between 34 to 35% of SL in the other three species.

Eye Diameter.—Proportionate size of the eye is not significantly different among the developmental stages. Eye size averages slightly larger in *P. arafurensis*, ca. 43% of HL, and *P. cyanophrys*, 42% of HL, than in the other three species, which averages between 37 to 39% of HL.

Snout Length.—*Psenes* has a bluntly rounded snout, particularly on postflexion specimens. There is a suggestion of an inverse relationship between eye size and snout length. Snout length averages approximately 20% of HL in *P. arafurensis* and *P. cyanophrys*, 22% in *P. pellucidus*, 23% in *P. maculatus*, and 24% of HL in *P. sio*.

Snout to Anus.—Although the range in length from snout to anus is 46 to 59% of SL on postflexion larvae for the genus as a whole, the range for any given species is usually only about one-half as much. The snout-anus distance averages least on *P. pellucidus*, about 49% of SL, most on *P. maculatus* and *P. cyanophrys*, between 54 to 55% of SL, and intermediate on *P. arafurensis* and *P. sio*, between 51 and 52% of SL.

Body Depth at Pectoral Fin Base.—Postflexion larvae and juveniles of *Psenes* are relatively deep-bodied. For three species

Table 35. Body proportions of five species of *Psenes*, expressed as percentage of standard length (SL) or head length (HL)

Species and stage	Size range (mm)	Snout to anus/SL	Head length/SL	Eye diameter/HL	Snout length/HL	Depth at P base/SL	Sn-D/SL	Sn-A/SL	Sn-V/SL
Psenes arafurensis									
Preflexion	3.2 NL	43	22	47	28	26	-	-	32
Flexion	4.6- 4.9 NL	49-54	29-33	36-41	24-27	33-44	34-35	50-56	30-31
Postflexion	6.5-20.5 SL*	49-54	32-36	41-46	17-23	48-57	35-38	50-58	32-37
Psenes cyanophrys									
Preflexion	2.8- 3.3 NL	48-54	24-27	39-42	18-25	24-29	-	-	36-43
Flexion	3.9- 4.2 NL	51	33	37	23-26	39-41	38	53-54	31-34
Postflexion	4.8-19.1 SL	50-59	31-39	37-47	18-26	44-55	36-40(44)	52-61	33-38
Psenes maculatus									
Flexion	3.8 NL	47	29	36	25	32	34	-	26
Postflexion	6.7-22.8 SL	52-57	33-37	34-41	20-26	45-52	33-40	52-59	28-38
Psenes pellucidus									
Preflexion	3.8- 4.6 NL	39-45	24	37-40	22-25	20-24	-	-	33-37
Flexion	5.2- 5.9 NL	46-47	29	37-38	24-25	32-33	30-35	49-50	31-34
Postflexion	9.7-26.7 SL	46-53	27-33	35-44	18-25	43-57	27-34	48-55	29-35
Psenes sio									
Preflexion	3.2- 3.6 NL	42-50	22	38-43	22-25	20-25	-	-	31-38
Flexion	4.2- 5.5 NL	43-52	31-36	33-40	19-25	31-43	35-38	47-55	29-36
Postflexion	6.0-22.1 SL	46-53	29-35	32-42(56)	22-28	37-45	30-38	47-55	29-34

* Postflexion may include both larvae and early juveniles

(*P. arafurensis*, *P. cyanophrys*, and *P. pellucidus*), body depth at pectoral fin base averages 50% or more of SL, and it is only slightly less for *P. maculatus* (48% of SL). Only *P. sio* is moderately slender with body depth averaging slightly less than 41% of SL.

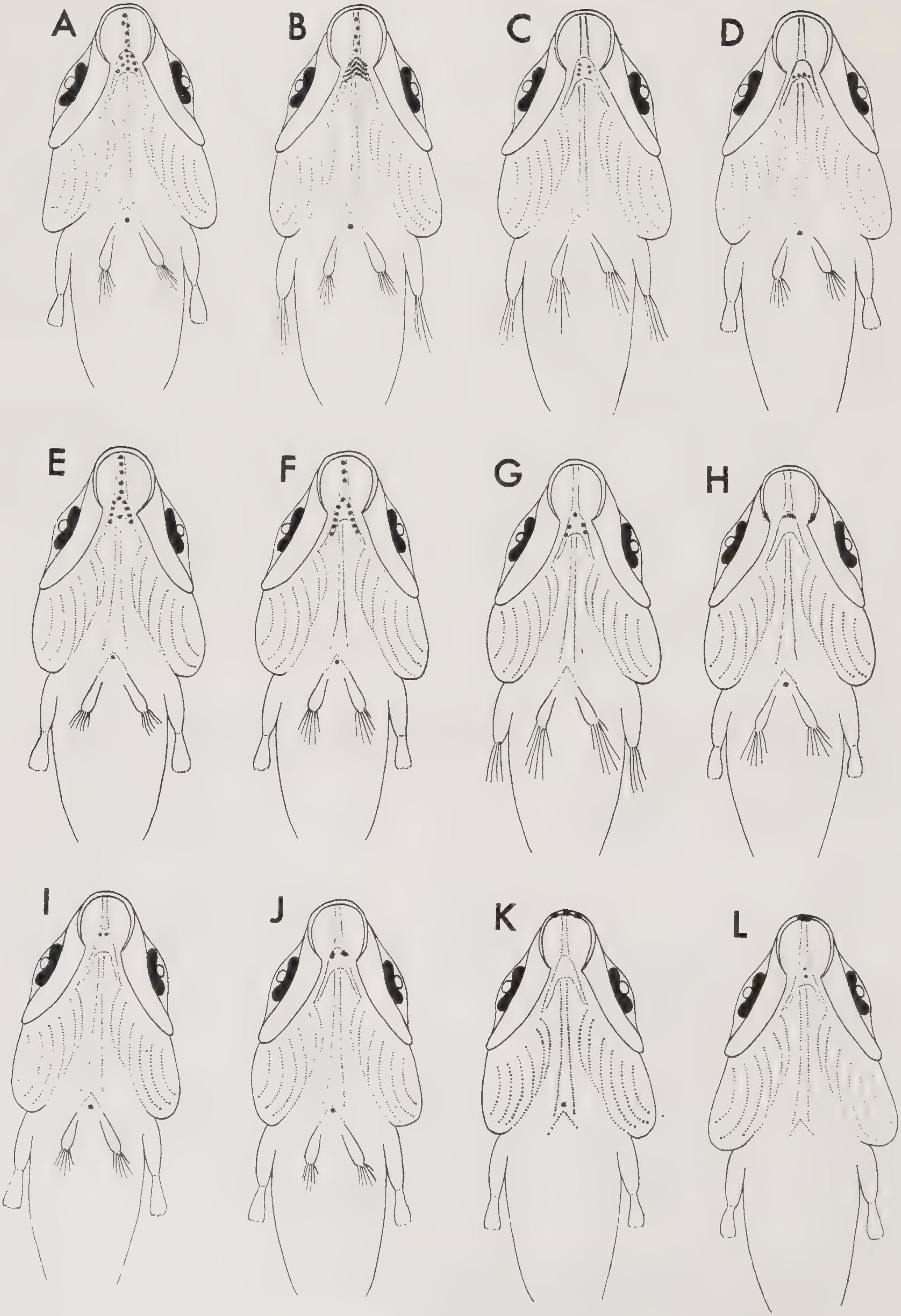
Snout to Dorsal Fin Origin.—This length is least for *P. pellucidus*, ca. 30% of SL, averages 34% of SL for *P. sio*, between 36 and 37% for *P. arafurensis* and *P. maculatus*, and over 38% for *P. cyanophrys*.

Snout to Anal Fin Origin.—The origin of the anal fin is close to the vent; the distance between the two seldom differ by more than about 2% of SL. This average difference for each species is approximately 2% greater than the value given under "Snout to Anus."

Snout to Insertion of Pelvic Fins.—Among the five species of *Psenes*, snout to pelvic fin insertions average between 28 to 38% of SL. For all species of *Psenes* except *P. pellucidus*, this value is slightly less than that for snout to dorsal fin origin.

Comparative Pigmentation

In all species of *Psenes*, the pelvic fins which form early on preflexion larvae are partially or wholly pigmented. Preflexion larvae of all species of *Psenes* dealt with (except *P. cyanophrys*) have a row of ventral midline pigment spots posterior to the vent, usually spaced one per myomere. These spots are best developed on preflexion specimens; by late preflexion and during flexion the spots become embedded and appear to move dorsad and usually persist to early postflexion. Larvae of all species of *Psenes* that were examined have a lateral line patch of pigment on the tail spaced about midway between the termination of the gut and the tip of the notochord, usually with opposing dorsal and ventral margin patches. This pigment area is developed on preflexion larvae and is retained throughout the larval period with augmentation. In addition, lar-


A
B
C
D
E
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G
H
I
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K
L

vae of *Psenes* have pigment on the ventral margin of the notochord near its tip on preflexion larvae, which becomes a patch over the hypural bones on flexion and postflexion larvae.

All species of *Psenes* lack pigment on top of the head on preflexion larvae. Pigment on the head begins to form above the eyes during flexion. Pigment on the upper jaw forms on late preflexion or early flexion stage larvae. The characteristic head pigment on preflexion larvae of *Psenes* is that under the lower jaw. This is shown in a series of illustrations of the ventral side of the head and trunk of five species of *Psenes* and two species of *Cubiceps* (Fig. 29). The figures are semi-diagrammatic in that the same basic body form is used for all species. However, each pigment pattern with consequent changes on the underside of the head are unique to each specimen illustrated.

Four illustrations are included of *Psenes pellucidus* (A to D). The lower jaw pigment is best developed on preflexion larvae, as is shown for a 4.2-mm specimen (A), is still heavy on the 5.7-mm early postflexion specimen (B), but is much reduced on the 9.7-mm postflexion specimen (C). Interestingly, Atlantic material of *Psenes pellucidus* lacked the forward anterior-posterior line of pigment under the jaw on a preflexion specimen (D).

Somewhat similar ventral jaw pigment is developed on larvae of *Psenes sio*, in the form of an inverted Y; it is well developed on a 3.8-mm preflexion specimen (E) and on an early postflexion specimen, 5.8 mm (F), but is much reduced on a 6.5-mm postflexion specimen (G).

In contrast to the heavy jaw pigment developed on preflexion specimens of *P. pellucidus* and *P. sio*, only a cluster of a few spots are developed on preflexion larvae of *P. arafurensis* (H) and only two spots on preflexion larvae of *P. cyanophrys* (I) and *P. maculatus* (J).

All five species of *Psenes* have a pigment spot developed behind the cleithral symphysis on preflexion larvae, which is lost during the postflexion stage.

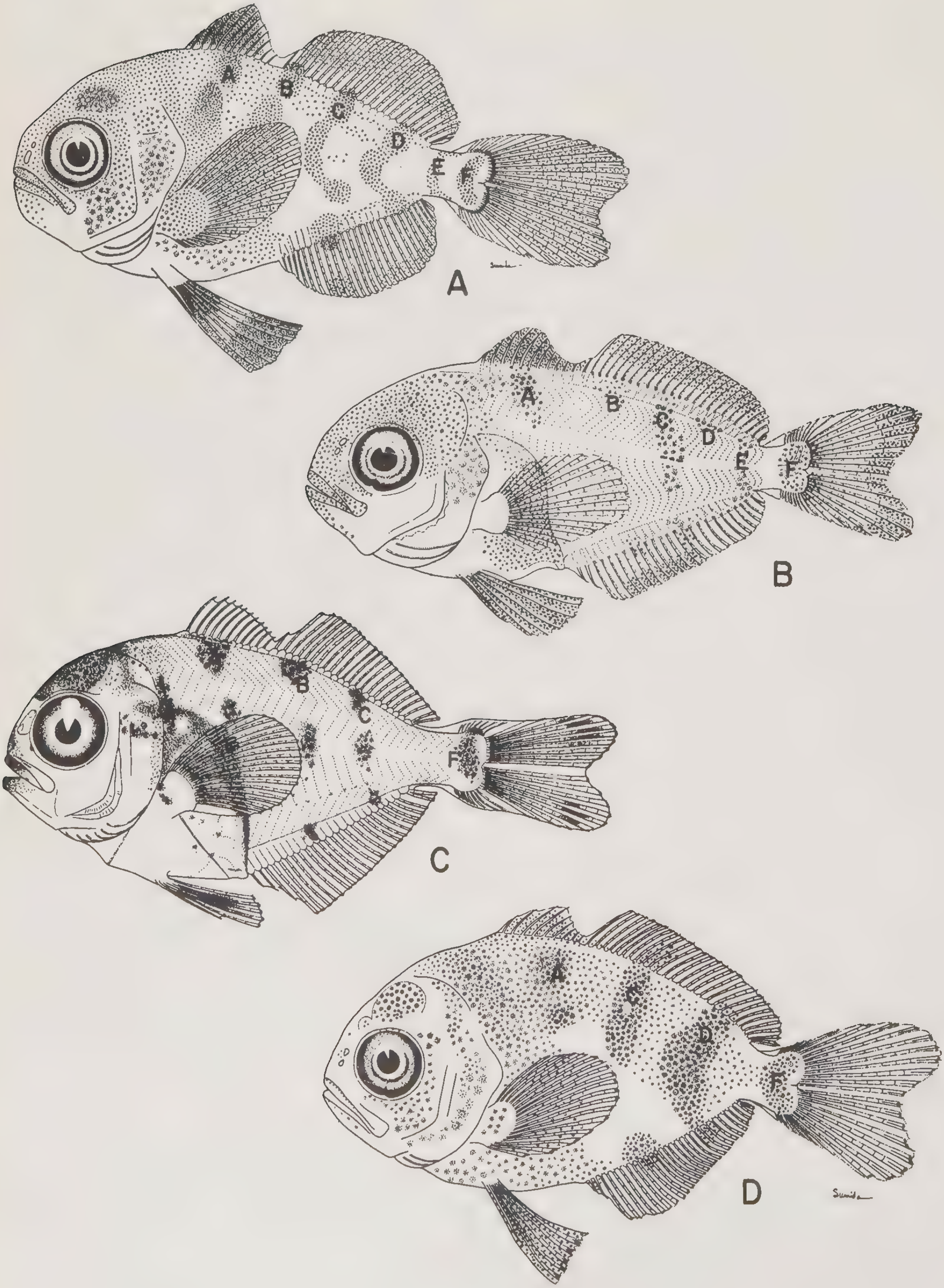
The ventral head pigment is sparse on preflexion larvae of *Cubiceps*. In the 3.8-mm preflexion specimen of *C. pauciradiatus* (K), the only ventral head pigment is on the tip of the lower jaw. The spot at the cleithral symphysis is anterior to it, not posterior as in *Psenes*. Preflexion larvae of *C. caeruleus* (L) lack the spot at the cleithral symphysis but have two ventral head spots forward of the isthmus and pigment on the tip of the lower jaw.

On postflexion larvae and early juveniles of *Psenes*, pigment develops in patches or streaks on the body. Most of the pigment streaks extending across the body develop from three centers of pigmentation; a dorsal, a lateral and a ventral center. Pigment is most heavily developed on late larvae and early juveniles of *P. cyanophrys*, least developed on *P. pellucidus* and intermediate on the other three species. Differences in patterns of pigmentation with increase in size are discussed under the individual species of *Psenes*. However, we were struck by the similarity in pigment patches that develop on the body of late postflexion and early juvenile specimens of *Psenes*, as is shown in Figure 30.

The pigment patches on the body are strikingly shown on a 22.2-mm specimen of

←

Figure 29. Semi-diagrammatic sketches of ventral head and cleithral pigment patterns of early stages of five species of *Psenes* and two species of *Cubiceps*. A—*Psenes pellucidus*, 4.2-mm preflexion larva; B—*P. pellucidus*, 5.7-mm postflexion larva; C—*P. pellucidus*, 9.7-mm postflexion larva; D—*P. pellucidus*, 4.2-mm preflexion larva, Atlantic specimen; E—*P. sio*, 3.8-mm preflexion larva; F—*P. sio*, 5.8-mm postflexion larva; G—*P. sio*, 6.5-mm postflexion larva; H—*P. arafurensis*, 3.3-mm preflexion larva; I—*P. cyanophrys*, 4.4-mm preflexion larva; J—*P. maculatus*, 3.8-mm preflexion larva, Atlantic specimen; K—*Cubiceps pauciradiatus*, 3.8-mm preflexion larva; L—*C. caeruleus*, 3.7-mm preflexion larva.


A
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Sumida

Psenes maculatus (Atlantic) (Figure 30A), which we are labelling A to F. Pigment-patch A develops under the middle of the first dorsal fin, pigment-patch B at the beginning of the second dorsal fin, pigment-patch C in the middle of the second dorsal fin, pigment-patch D near the posterior end of the second dorsal fin, pigment-patch E on the caudal peduncle and pigment-patch F over the hypural plates. The dorsal and lateral patches are still separate for A and B and the ventral patch is separate for C.

There are six dorsal patches developed on a 17.4-mm specimen of *P. sio* (Fig. 30B), that correspond almost precisely to those on *P. maculatus*. The only difference is in the more anterior placement of patch E so that it comes under the terminal rays of the second dorsal fin rather than behind it.

The two species with fewer vertebrae, *P. arafurensis* and *P. cyanophrys*, develop four patches. In an 11.0-mm specimen of *P. arafurensis* (Fig. 30C), the patches correspond to A, B, C and F on *P. maculatus* and are thus labelled. The four pigment patches on an 11.7-mm specimen of *P. cyanophrys* from the Atlantic (Fig. 30D) correspond to patches A, C, D and F of *P. maculatus*. Usually larvae of this size of *P. cyanophrys* are more heavily pigmented over the body but with the pigment patches persisting as intensified areas of pigmentation.

Body pigment develops more gradually on juveniles of *P. pellucidus*, but the six primary areas can be identified, even though additional patches fill in between them on larger specimens.

Psenes arafurensis
Günther, 1889
Figures 31 to 33

Literature.—The only previous record of *Psenes arafurensis* from the eastern Pacific was by Fowler (1928) from the Hawaiian Islands.

Material.—Larvae and early juveniles were examined from the plankton collections from EASTROPAC cruises, and 14 pelagic trawl collections from later cruises in the same area. In addition, larvae and early juveniles were examined from off Hawaii and from several localities to the north of Hawaii.

Distribution.—This species was widely distributed offshore between 10°N and 10°S in the eastern tropical Pacific (Fig. 34). It was quite common near Hawaii and was taken to about 32°N in the central water mass (Fig. 18).

Distinguishing Characters.—JUVENILES. This species can be distinguished from other *Psenes* by meristics, morphometrics and pigmentation. The combination of low total vertebral count (31) and low dorsal (X to XI, I, 20 to 23) and anal fin (III, 21 to 23) counts separates it from its congeners (Table 1). Early juveniles of *P. arafurensis* (Figs. 32B, C) are deeper bodied and less heavily pigmented than comparable-sized specimens of *P. cyanophrys*.

LARVAE. Preflexion larvae have a line of ventral pigment spots, a character that separates them from preflexion larvae of *P. cyanophrys*. They lack the pigment under the head found on preflexion *P. sio* and *P. pellucidus*. They resemble larvae of *P. maculatus* but preflexion stage larvae can be separated by myomere counts (31 vs. 35), and later stage larvae by differences in pigment patterns.

Meristics.—Vertebrae 12 + 19 = 31 (rarely 12 + 20 = 32); first dorsal X or XI (average 10.9); second dorsal I, 20 to 22 (23) (average I, 21.1); anal III, 21 to 23 (average III, 22.4); principal caudal rays 9 + 8; secondary caudal rays 7 to 10 dorsal + 7 to 10 ventral (average 8.1 + 8.3).

Meristics of 25 specimens from about 4°S to about 28°N and from about 96°W

←

Figure 30. Composite view of four species of *Psenes*, showing similarities in patterns of body pigment patches. Pigment areas labelled A to F are explained in the text. A—*P. maculatus*, 22.2 mm (Atlantic specimen); B—*P. sio*, 17.4 mm (Pacific specimen); C—*P. arafurensis*, 11.0 mm (Pacific specimen); D—*P. cyanophrys*, 11.7 mm (Atlantic specimen).

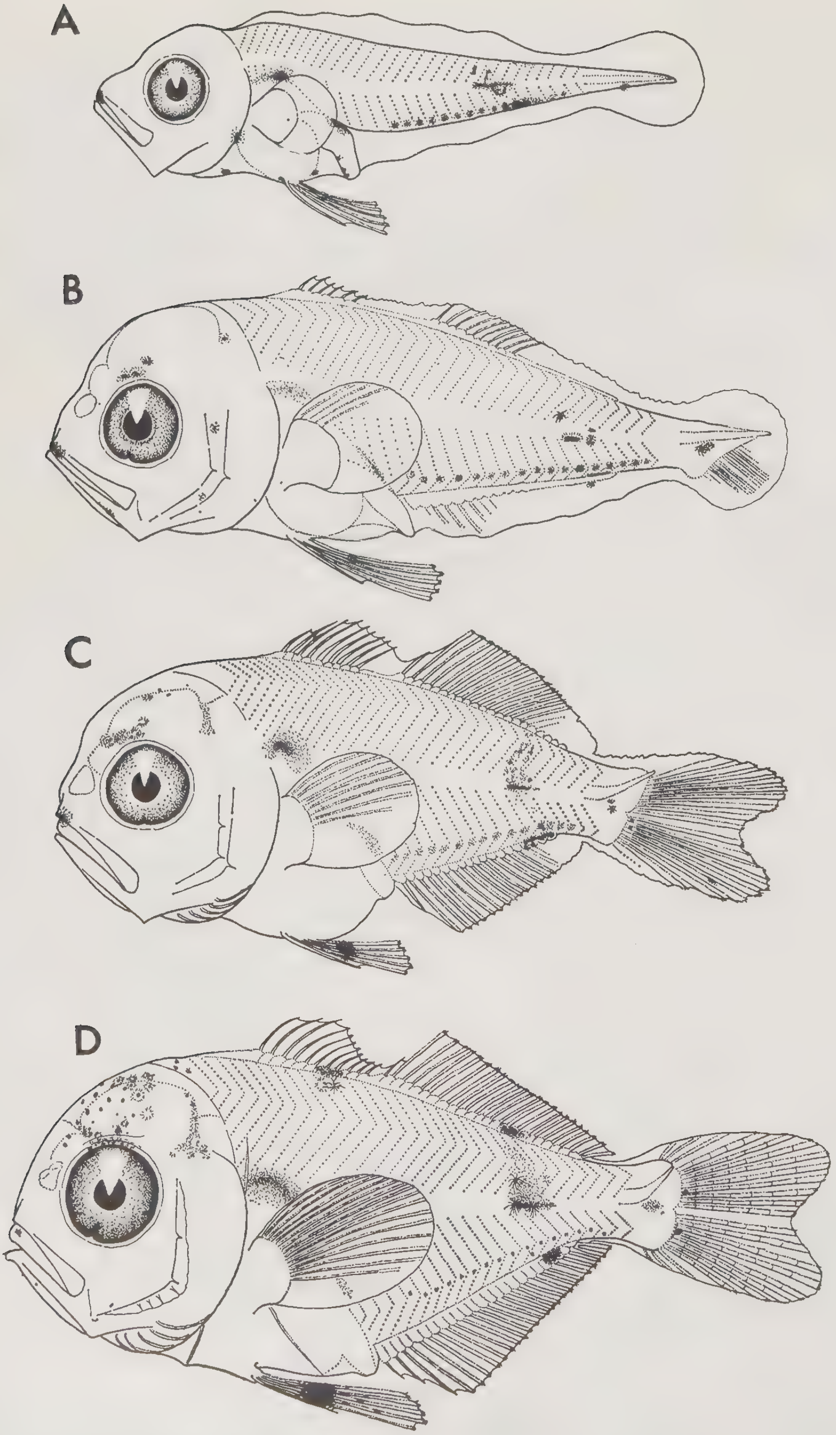

Figure 31. Developmental stages of *Psenes arafurensis* (Nomeidae). A—3.2-mm preflexion larva; B—4.9-mm early flexion larva; C—4.6-mm late flexion larva; D—6.5-mm postflexion larva.

Table 36. Meristics of 25 juveniles of *Psenes arafurensis* from over its distributional range in the eastern Pacific, including off Hawaii (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Aries 9	27°34.6'N	155°39.7'W	X.5.71	17.4	12+19=31	X	I,22	III,23	8-17-8
T.C. 32.012	21°23'N	158°15'W	VII.16.67	36.5	12+19=31	X	I,20	III,21	8-17-8
"	"	"	"	47.3	12+19=31	XI	I,20	III,23	8-17-8
T.C. 32.055	21°23'N	158°15'W	VIII.23.67	117.0	12+19=31	XI	I,22	III,23	8-17-8
T.C. 32.002	21°22'N	158°12'W	VII.12.67	47.5	12+19=31	XI	I,20	III,22	8-17-8
"	"	"	"	62.0	12+19=31	XI	I,21	III,21	9-17-8
T.C. 32.008	21°22'N	158°16'W	VII.14.67	69.0	12+19=31	XI	I,21	III,22	9-17-9
"	"	"	"	73.5	12+19=31	XI	I,21	III,23	9-17-8
Jord. 57.053	09°51.4'N	117°32.5'W	XI.16.70	29.0	12+19=31	XI	I,22	III,23	7-17-8
T.C. 51.018	07°44'N	118°53'W	XI.3.70	12.0	12+19=31	XI	I,22	III,23	9-17-9
"	"	"	"	12.5	12+19=31	XI	I,20	III,21	8-17-8
Jord. 57.112	07°00'N	119°20'W	XII.7.70	15.0	12+19=31	XI	I,20	III,21	9-17-9
"	"	"	"	16.5	12+19=31	XI	I,21	III,22	7-17-7
ETP 11.068	06°05'N	118°51'W	II.3.67	12.5	12+20=32	XI	I,21	III,23	8-17-8
Jord. 77.101	04°21.5'N	118°14.8'W	I.28.73	12.4	12+19=31	X	I,23	III,23	9-17-10
Jord. 65.208	00°30'S	96°13'W	IX.27.71	20.0	12+19=31	XI	I,21	III,23	7-17-7
Jord. 60.046	01°43'S	118°58'W	XII.27.67	20.5	12+19=31	XI	I,21	III,22	7-17-8
T.C. 51.056	03°12'S	119°26'W	XI.10.70	18.4	12+19=31	XI	I,21	III,22	9-17-9
"	"	"	"	27.9	12+19=31	XI	I,21	III,22	7-17-8
Jord. 77.054	03°40'S	118°39'W	I.19.73	50.5	12+19=31	XI	I,21	III,23	8-17-8
T.C. 51.063	03°44'S	119°30'W	XI.12.70	44.0	12+19=31	XI	I,21	III,22	7-17-7
"	"	"	"	49.0	12+19=31	XI	I,21	III,21	7-17-7
"	"	"	"	52.0	12+19=31	XI	I,21	III,21	8-17-9
T.C. 51.048	04°02'S	118°48'W	XI.8.70	35.5	12+19=31	XI	I,21	III,23	8-17-8
"	"	"	"	40.0	12+19=31	XI	I,21	III,22	8-17-8

to about 158°W are given in Table 36. No geographical variation of any count is indicated.

Morphometrics.—Morphometrics of a developmental series are presented in Table 37. Body proportions are discussed in the "Comparative Morphometrics" section of *Psenes.*

Ossification.—The pelvic fins are first to develop after the larval pectoral fins, as is characteristic for *Psenes* larvae. The smallest available specimen, 3.0 mm, already has pelvic fins with I, 5, the full count.

Due to a limited amount of material, small larvae could not be cleared and stained, so information on early fin formation is based on careful examination of small larvae used for illustrations. A 4.9-mm specimen just prior to the beginning of notochord flexion has rays and/or spines developing in the first and second dorsal, anal, caudal, and pectoral fins (Fig. 31B). A more advanced flexion larva of 4.6 mm (Fig. 31C) has all 9 + 8 principal caudal rays and a first dorsal fin short of only two spines. By 6.5 mm (Fig. 31D) the first dorsal, second dorsal, and anal fins are fully formed. The pectoral fins acquire all their rays (18 to 21) by 8.0 mm, and the caudal fin by 9.8 mm (Table 38).

A detailed study of vertebral ossification could not be made due to lack of small cleared and stained specimens. All 31 vertebrae (12 + 19) are ossifying by 8.0 mm, the smallest size larva that was cleared and stained (Table 38).

Branchiostegal rays form early with 0 + 4 counted on a 3.2-mm preflexion larva and the full complement of 2 + 4 present on a 4.9-mm early flexion larva. Gill rakers on the first arch are not evident on a 3.2-mm larva, but can be seen on the lower limb in a 4.9-mm larva. The adult number of gill rakers (8 + 1 + 15 to 17) is formed by 20.3 mm (Table 38).

Table 37. Morphometrics, in mm, of larvae and juveniles of *Psenes arafurensis* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 11.114	3.2 NL	1.4	0.72	0.34	0.20	0.82	-	-	1.0
ETP 75.239	4.9	2.4	1.4	0.50	0.34	1.6	1.7	2.4	1.5
ETP 11.066	4.6	2.5	1.5	0.62	0.40	2.0	1.6	2.6	1.4
Hawaii 71-10-3	6.5 SL	3.4	2.2	1.0	0.48	3.1	2.4	3.6	2.4
"	6.7	3.5	2.2	0.92	0.44	3.2	2.6	3.6	2.3
"	6.9	3.4	2.3	1.0	0.44	3.6	2.6	3.6	2.2
'	7.9	4.1	2.6	1.1	0.56	3.9	2.7	4.2	2.6
"	8.0	4.2	2.6	1.1	0.52	4.2	3.0	4.2	2.7
ETP 11.068	8.0	4.1	2.9	eyes gone	0.60	4.3	2.9	4.3	2.7
Hawaii 71-10-3	8.6	4.6	3.0	1.2	0.56	4.4	3.3	4.6	2.9
"	11.0*	5.5	3.5	1.6	0.60	5.8	3.8	5.5	3.5
ETP 13.079	12.2*	6.5	4.2	1.9	0.75	6.8	4.7	6.8	4.3
Jord. 77.101	12.4*	6.7	4.2	1.8	0.83	7.0	4.3	7.2	4.2
T.C. 51.056	18.4*	9.4	6.4	2.9	1.2	10.2	6.5	9.7	5.8
T.C. 51.071	20.5*	10.4	6.7	2.8	1.4	11.7	7.7	10.7	6.8
T.C. 51.056	22.9*	16.7	10.5	4.7	2.2	15.0	10.5	17.7	11.2

* Juvenile

A few small spines develop along the margin and ridge of the preopercle on larvae between 4.5 and 9.0 mm. These weakly developed spines become embedded in a fringe-like membrane along the preopercular margin in specimens up to ca. 11.5 mm when they are completely resorbed.

Teeth are not evident in larvae until ca. 6.5 mm. An 8.0-mm larva has four premaxillary and two dentary teeth, and more are added with increasing size (Table 38).

Scales first appear below the pectoral fin base on an 8.0-mm larva, but this specimen has only 6 + 6 secondary caudal fin rays. A 9.8-mm specimen has scales extending over the ventral portion of the abdomen in addition to having 10 + 10 secondary caudal rays and ray formation in all other fins completed, thus qualifying it as an early juvenile.

Pigmentation.—The most conspicuous pigment of early larvae is a line of ventral spots on the tail (Fig. 31A to D). This pigment becomes embedded in postflexion larvae and subsequently disappears (Fig. 32). Body pigment on postflexion larvae and early juveniles forms as distinct dorsal, lateral, and ventral patches which merge into conspicuous bands (Figs. 32 and 33).

Preflexion larvae are lightly pigmented. The smallest specimen, 3.2 mm, lacks pigment on top of the head and under the lower jaw; some pigment is present on the upper

Table 38. Meristics of a cleared and stained postflexion larva and of juveniles of *Psenes arafurensis*

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
Hawaii 7-10-3	8.0 SL	XI	I,21	III,23	20	I,5	6-9+8-6	12+19=31	2+4	3+1+11	4	2
Jord. 57.113	9.8*	XI	I,20	III,23	18	I,5	10-9+8-10	12+19=31	2+4	4+1+12	6	6
T.C. 32.012	11.4*	XI	I,21	III,23	21	I,5	8-9+8-9	12+19=31	2+4	6+1+13	6	7
ETP 13.079	12.2*	XI	I,22	III,23	20	I,5	7-9+8-8	12+19=31	2+4	6+1+11	6	6
T.C. 32.010	13.4*	XI	I,21	III,23	20	I,5	8-9+8-9	12+19=31	2+4	7+1+14	8	8
T.C. 51.071	20.3*	XI	I,21	III,23	20	I,5	8-9+8-8	12+19=31	2+4	8+1+15	7	7
T.C. 32.012	23.2*	XI	I,22	III,23	21	I,5	9-9+8-10	12+19=31	2+4	8+1+17	8	11

* Juvenile

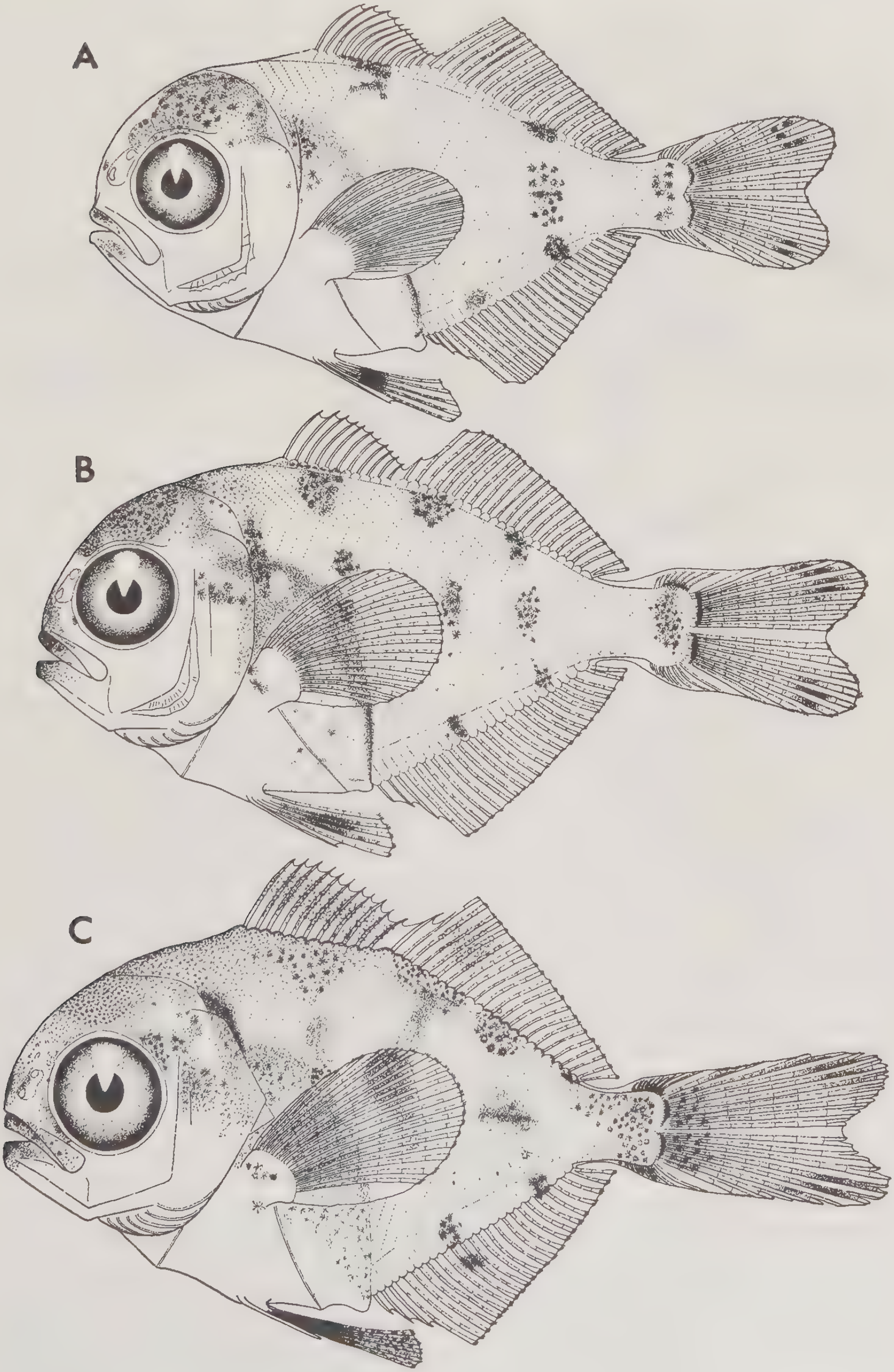

Figure 32. Developmental stages of *Psenes arafurensis* (Nomeidae). A—8.6-mm postflexion larva; B—11.0-mm early juvenile; C—18.4-mm early juvenile.

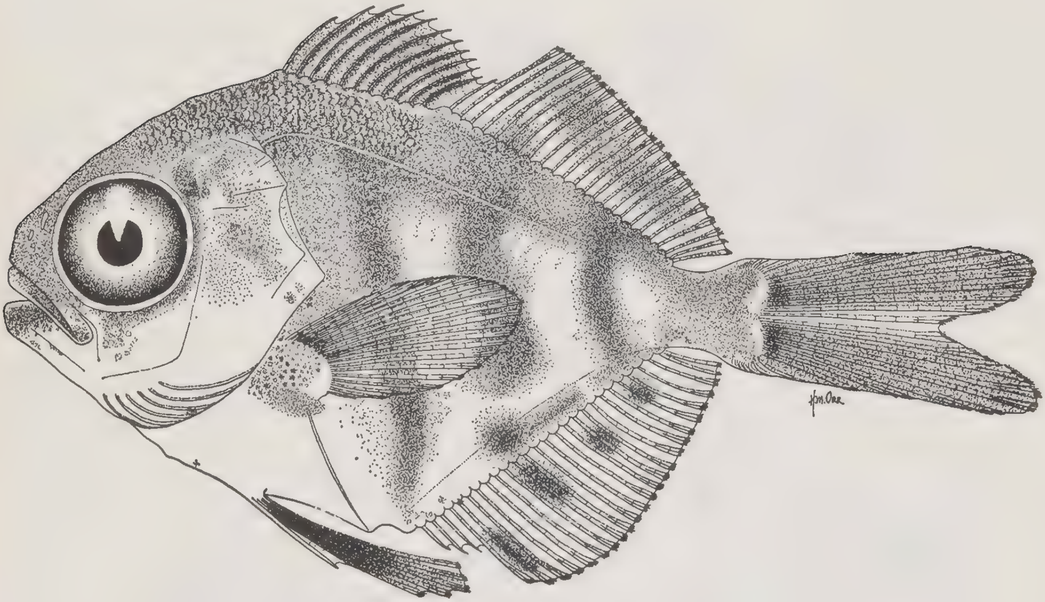

Figure 33. Early juvenile of *Psenes arafurensis* (Nomeidae), 30.0 mm.

jaw and embedded on the peritoneum (Fig. 31A). A melanophore is present near but posterior to the cleithral symphysis (Fig. 29H), one or two melanophores are present near the pelvic fins, and several are on the downturned gut forward of the anus. Body pigment consists of a series of about 15 melanophores spaced one per myomere along the ventral margin of the tail. Pigment ventrad of the tip of the notochord and that along the lateral line between about myomeres 21 to 25 will become prominent patches in later larvae.

Flexion larvae add pigment on the head above the eyes, over the hypurals, at the base of the developing caudal rays, and on the pelvic fins (Figs. 31B and C). The row of ventral pigment spots is still conspicuous. Pigment is lacking posterior to the cleithral symphysis and under the abdomen. Lateral line pigment at myomeres 22 to 25 spreads dorsally, an opposing ventral pigment patch forms at the base of the developing anal fin, but no opposing pigment patch has formed as yet on the dorsal margin.

Postflexion larvae and early juveniles (Figs. 31D and 32A to C) lose some of the pigment of earlier stages and develop the banded pigment pattern characteristic of the genus. Pigment intensifies on the upper jaw, on the head above the eyes, and later (11.0 mm) behind the eyes as well. Pigment forms on the lower jaw at about 8.6 mm. On the tail, the ventral line of pigment spots moves internally and disappears by 8.6 mm. The lateral line pigment gradually merges with opposing dorsal and ventral pigment to form a vertical band across the tail at about myomeres 21 to 25. A band of pigment begins developing on 6.5-mm larvae below the first dorsal fin at the base of the seventh and eighth spines. It increases in size in later stages and extends ventrally. By 11.0 mm (Fig. 32B) another dorsal patch forms under the anterior rays of the second dorsal fin midway between the two dorsal patches already characterized. Lateral and ventral pigment patches form under this middle patch, and a lateral patch also forms under the anterior dorsal patch. The pigment near

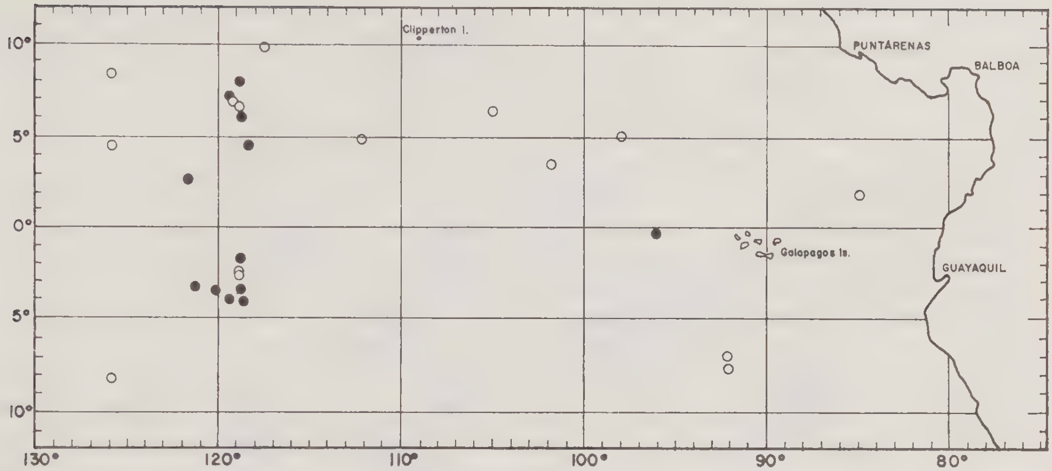

Figure 34. Occurrences of *Psenes arafurensis* larvae (open circles) and juveniles (closed circles) in the eastern tropical Pacific.

the tip of the notochord on preflexion larvae intensifies into a broad patch over the hypural bones and becomes conspicuous along the base of the caudal fin (Figs. 32A to C). A pigment patch develops near the outer margin of each of the two caudal fin lobes (by 8.6 mm, Fig. 32A). Pigment gradually forms externally over the abdominal cavity and also spreads backwards from the head to the nape (by 11.0 mm, Fig. 32B). The dorsal, anal, and pectoral fins lack pigment on this 11.0-mm specimen, which is probably an early juvenile. Body and fin pigment becomes intensified on somewhat larger juveniles (Figs. 32C and 33). On the 18.4 mm specimen, the first dorsal fin is rather heavily pigmented; the second dorsal fin is pigmented between the seven anterior rays, whereas the only pigment on the anal fin is a small patch spreading out from the anterior-most ventral patch at rays 8 to 10. The pelvic fins are now completely pigmented and the caudal fin pigment has intensified along the fin base and distally on the dorsal and ventral lobes.

On a 30.0-mm juvenile (Fig. 33) pigment is continuous along the back and in the three vertical bands on the body. All the fins are more heavily pigmented, with four distinct pigment patches on the anal fin and almost continuous pigment over much of the second dorsal fin.

Psenes cyanophrys
Cuvier and Valenciennes, 1833
Figures 35 to 37

Literature.—Three previous records from the eastern Pacific by Meek and Hildebrand (1925) and Hunter and Mitchell (1967 and 1968) referred to *P. pacificus* Meek and Hildebrand (1925) which was synonymized with *P. cyanophrys* by Haedrich (1967). It is recorded as *P. cyanophrys* by Gooding and Magnuson (1967) and Parin (1968). *Psenes kamokari*, described by Abe, Kojima and Kosakai (1963) from Kyushu in the western Pacific also is considered a synonym by Haedrich (1967).

Interestingly, it was the only nomeid recorded by Hunter and Mitchell (1967 and 1968) and ranked second in numbers of fishes captured beneath their moored rafts off Costa Rica. EASTROPAC collections, however, indicate that larvae of *P. sio* and *Cubiceps pauciradiatus* are much more common in this area than are those of *P. cyanophrys.*

In similar experiments using a floating raft with an underwater chamber, Gooding and Magnuson (1967) found that *P. cyanophrys* was the first fish to appear, attained the highest rate of accumulation and abundance in three central Pacific localities: off the leaward coast of the island of Hawaii, at the equator, and at ca. 3°S between about 148° to 159°W.

A life history series was illustrated by Legaspi

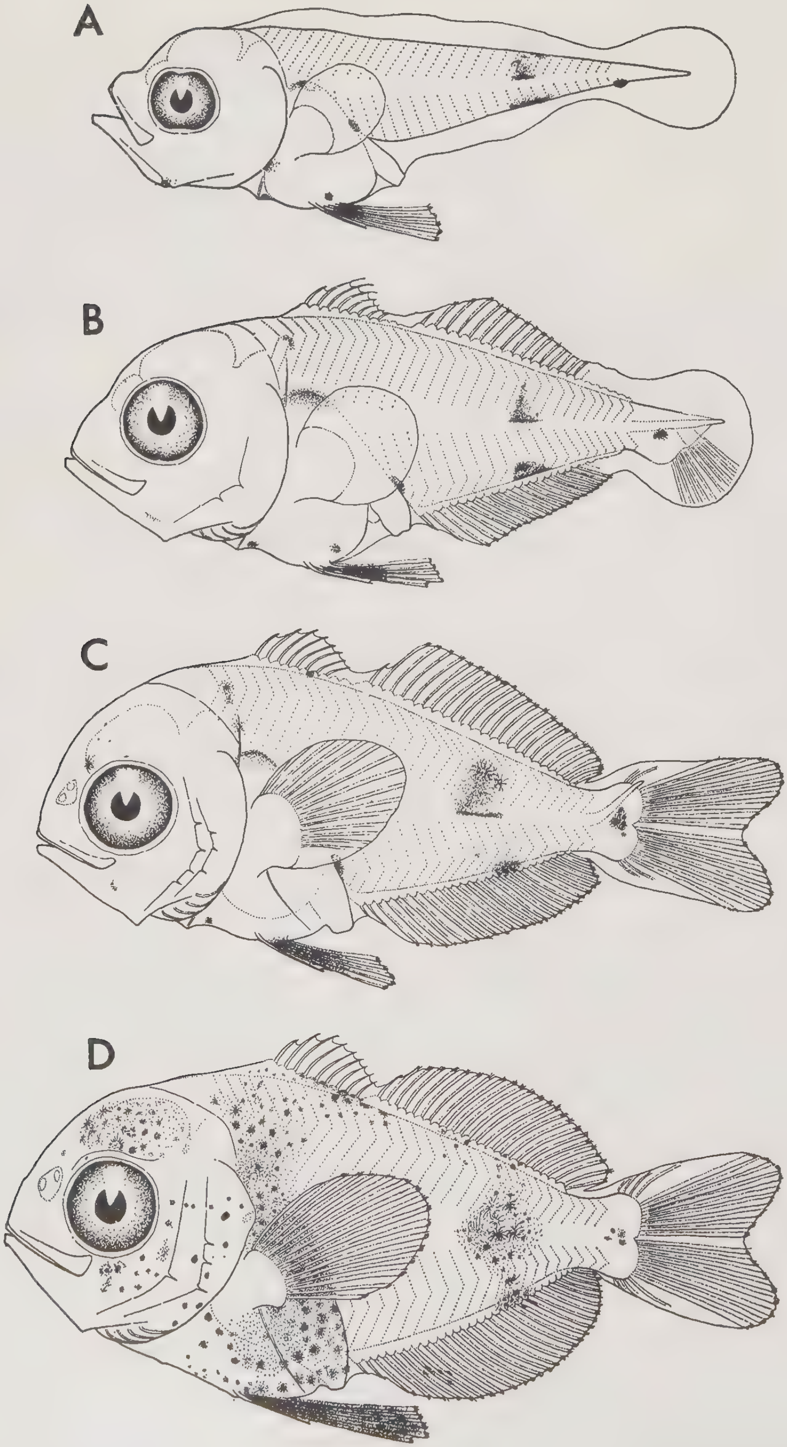

Figure 35. Developmental stages of *Psenes cyanophrys* (Nomeidae). A—3.3-mm preflexion larva; B—4.2-mm early flexion larva; C—5.0-mm postflexion larva; D—6.8-mm postflexion larva.

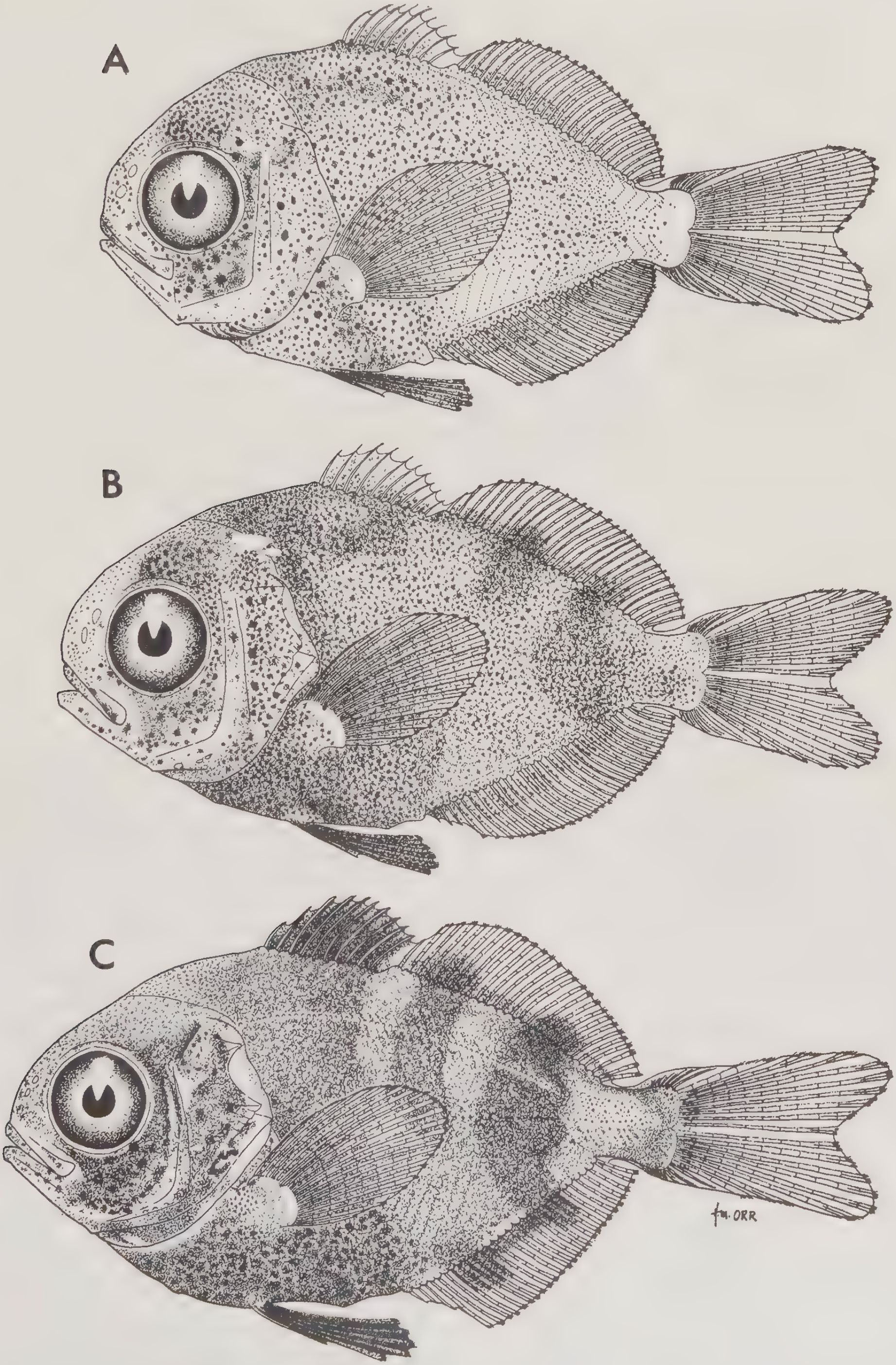

Figure 36. Developmental stages of *Psenes cyanophrys* (Nomeidae). A—10.7-mm early juvenile; B—14.5-mm early juvenile; C—19.1-mm juvenile.

Table 39. Meristics of 25 juveniles of *Psenes cyanophrys* selected from over its distributional range in the eastern Pacific, including off Hawaii (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
T.C. 32.005	21°22'N	158°13'W	VII.13.67	33.2	12+19=31	X	I,25	III,25	8-17-8
T.C. 32.008	21°22'N	158°16'W	VII.14.67	27.8	12+19=31	X	I,25	III,24	8-17-7
T.C. 32.015	21°20'N	158°12'W	VII.17.67	40.4	12+19=31	X	I,25	III,25	9-17-9
Hawaii 71-6-18	21°00'N	158°20'W	VI.16.71	13.3	12+19=31	X	I,26	III,26	9-17-9
T.C. 32.024	20°59'N	158°30'W	VII.22.67	44.0	12+19=31	X	I,26	III,25	8-17-8
T.C. 32.028A	20°59'N	158°34'W	VII.25.67	37.8	12+19=31	X	I,25	III,25	8-17-8
SIO 64-141	10°32'N	85°54'W	X.21.63	51.0	12+19=31	IX	I,26	III,26	9-17-9
SIO 63-305	10°00'N	86°00'W	IV.2.63	31.8	12+19=31	IX	I,25	III,25	8-17-8
	"	"	"	40.0	13+18=31	X	I,26	III,24	8-17-8
SIO 63-307	10°00'N	86°00'W	IV.2.63	32.8	12+19=31	IX	I,26	III,26	9-17-9
SIO 63-313	9°49'N	85°31'W	IV.11.63	17.8	12+19=31	X	I,25	III,25	8-17-8
"	"	"	"	23.0	12+19=31	X	I,24	III,25	7-17-8
SIO 63-322	9°45'N	85°37'W	V.8.63	42.5	13+18=31	X	I,25	III,26	9-17-8
Hunter & Mitchell	9°45'N	85°39'W	IV.21.66	39.0	12+19=31	X	I,25	III,26	8-17-8
"	"	"	"	43.0	12+19=31	X	I,25	III,26	9-17-8
	"	"		46.0	12+19=31	X	I,26	III,25	8-17-8
Hunter & Mitchell	9°45'N	85°43'W	IV.13.65	42.0	12+19=31	IX	I,25	III,26	8-17-8
"	"	"	"	45.0	12+19=31	X	I,25	III,25	8-17-8
"	"	"	"	47.0	12+19=31	X	I,25	III,26	8-17-8
SIO 63-319	8°32'N	83°54'W	V.4.63	70.0	12+19=31	X	I,26	III,26	8-17-8
"	"	"	"	72.0	13+18=31	X	I,25	III,25	8-17-8
"	"	"	"	80.0	12+19=31	X	I,26	III,26	8-17-8
T.C. 51.018	7°44'N	118°53'W	XI.3.70	14.2	12+19=31	IX	I,26	III,26	7-17-7
Jord. 57.113	7°14.6'N	119°24'W	XII.7.70	19.2	12+19=31	X	I,25	III,25	7-17-7
"	"	"	"	25.7	12+19=31	X	I,25	III,25	8-17-8

(1956) from the Atlantic: Of the six illustrations only the two largest, 9.4 and 17.0 mm (Figs. 3E and F) are definitely *P. cyanophrys*, and the 4.7-mm specimen (Fig. 2C) is possibly this species. The 2.5-mm and 3.2-mm specimens (Figs. 2A and B) are possibly *Ariomma*, and the 6.9-mm specimen (Fig. 3D) appears to be a carangid.

Material.—Juvenile material was examined from off Costa Rica (Hunter and Mitchell, 1967 and 1968), from trawl collections made in the eastern tropical Pacific on cruises of the DAVID STARR JORDAN and TOWNSEND CROMWELL, and from Hawaii (TOWNSEND CROMWELL cruise 32). Larvae were obtained from EASTROPAC collections. Comparative material was examined from the Atlantic and from the Gulf of Thailand.

Distribution.—A moderate number of larvae were collected on EASTROPAC cruises between 0° and 10°N (Fig. 38). Juvenile material was abundant from collections made off Costa Rica and Hawaii. There is an obvious disproportion between the abundance of juveniles observed under floating objects, and the relative scarcity of larvae in plankton hauls.

Distinguishing Characters.—JUVENILES. Juvenile *P. cyanophrys* can be distinguished by meristics, pigmentation, dentition, and skeletal characters. The combination of 31 vertebrae and 23 to 26 anal rays is unique among nomeids (Table 1). Juveniles are more heavily pigmented at all stages than other *Psenes*. It is the only *Psenes* in the eastern Pacific with small pointed teeth in the lower jaw. A trenchant skeletal character is the position of the first haemal spine (on the 13th vertebra) in relation to the anal fin pterygiophores. In *P. cyanophrys* this haemal spine interdigitates between the fourth and fifth or the fifth and sixth anal pterygiophores. In other species of *Psenes*, this haemal spine interdigitates between the first and second or the second and third pterygiophores (Table 3).

LARVAE. Larvae of *P. cyanophrys* can be distinguished in all stages from other *Psenes* by pigmentation and in postflexion larvae by meristics. Preflexion and flexion stages

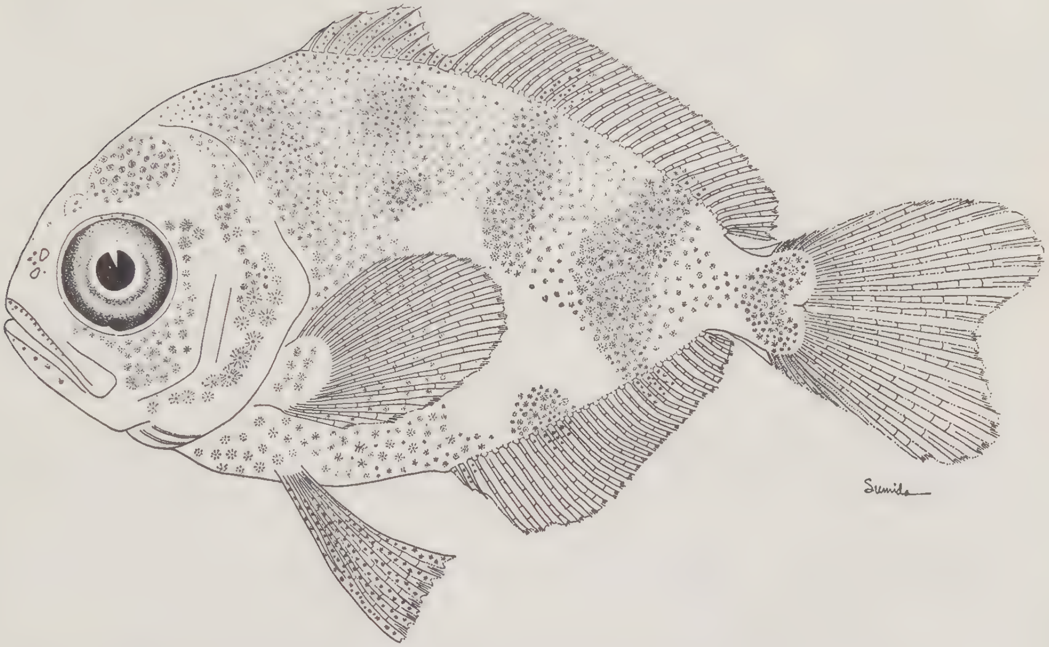

Figure 37. Early juvenile of *Psenes cyanophrys* (Nomeidae) from the Atlantic, 11.7 mm.

of *P. cyanophrys* differ from other *Psenes* in not having a line of melanophores on the ventral margin of the body behind the anus.

Postflexion larvae develop pigment bands at small sizes. The body soon becomes completely pigmented but the banding pattern persists against the background pigment.

Meristics.—Vertebrae 12 + 19 = 31 (rarely 13 + 18 = 31); first dorsal IX or X (average 9.8); second dorsal I, 23 to 26 (average I, 25.1); anal III, 23 to 27 (average III, 25.2); principal caudal rays 9 + 8; secondary caudal rays 7 to 9 dorsal + 7 to 9 ventral (average 8.1 + 7.9).

Meristics of 25 specimens from off Hawaii and from off Central America are given in Table 39. No difference in any count is indicated between the two areas.

Morphometrics.—Morphometrics of a series of *P. cyanophrys* are presented in Table 40. Body proportions are discussed in the comparative section of *Psenes* (Table 35).

Ossification.—As is typical for *Psenes* larvae, the pelvic fins are the first to develop in *P. cyanophrys*. The pelvic fins are present on the smallest available specimen of 2.7 mm, and a 3.6-mm cleared and stained larva has the full complement of I, 5 (Table 41). The first dorsal fin is next to start development which is the usual condition when a perciform larva develops precocious pelvic fins. A 3.6-mm preflexion larva has the anterior two spines formed (Table 41). By 4.2 mm, rays and spines are ossifying in the second dorsal, anal and caudal fins. A postflexion specimen of 4.7 mm has all fins complete except for the pectoral, some secondary caudal rays, and the anterior-most anal spine. The latter is formed by 6.9 mm, and the pectoral and secondary caudal rays are complete by 9.7 mm.

The axial skeleton develops early with the two anterior-most neural spines ossifying in a 3.6-mm preflexion larva; all 31 (12 + 19) vertebrae are formed in a 4.7-mm postflexion larva.

Table 40. Morphometrics, in mm, of larvae and juveniles of *Psenes cyanophrys* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 47.244	2.8 NL	1.5	0.68	0.28	0.12	0.66	-	-	1.2
ETP 13.056	3.0	1.5	0.80	0.34	0.20	0.86	-	-	1.1
ETP 13.052	3.3	1.6	0.88	0.34	0.20	0.90	-	-	1.2
ETP 75.241	3.9	2.0	1.3	0.48	0.30	1.6	1.5	2.1	1.2
ETP 13.241	4.2	2.2	1.4	0.52	0.36	1.6	1.6	2.3	1.4
ETP 20.100	4.8 SL	2.4	1.5	0.68	0.38	2.1	1.8	2.5	1.6
ETP 45.090	5.5	2.9	2.2	0.88	0.52	2.6	2.4	3.1	1.9
ETP 75.241	6.4	3.7	2.1	0.9[illegible]	0.52	3.4	2.6	3.8	2.1
Hawaii 71-9-3	7.8	4.4	2.7	1.[illegible]	0.44	3.9	2.8	4.6	2.7
ETP 14.209	9.7	5.3	3.4	1.6	0.60	4.9	3.7	5.6	3.6
Hawaii 71-9-3	10.7*	5.8	3.7	1.6	0.60	5.8	4.2	6.0	3.8
"	11.0*	6.1	3.7	1.8	0.75	5.9	4.2	6.4	3.9
"	11.7*	6.2	4.3	1.9	0.92	5.9	4.5	6.4	4.0
Hawaii 71-6-18	14.5*	7.6	5.0	2.2	0.91	7.3	5.4	7.9	4.9
Jord. 57.113	19.1*	11.0	7.2	2.7	1.4	10.5	7.7	11.7	7.0

* Juvenile

The complete set of 2 + 4 branchiostegal rays is formed by 4.7 mm at which time gill rakers, teeth and preopercular spines are evident. The largest cleared and stained specimen, 26.4 mm, still has an incomplete number of gill rakers. As with other *Psenes* larvae, the preopercular spines are small and inconspicuous. By 9.7 mm, they become embedded in a fringe of tissue and are completely resorbed after 17.0 mm.

Scales first appear on the shoulder region of a 10.0-mm specimen which has 8 + 8 secondary caudal rays developed; transformation from the larval to juvenile stage of *P. cyanophrys* is considered to occur at about this size.

Pigmentation.—Early larvae are sparsely pigmented and lack pigment spots along the ventral margin. Pigment is added rapidly after notochord flexion and soon becomes very heavy.

Preflexion larvae lack pigment on top of the head or the upper jaw (Fig. 35A). Pigment is present just behind the cleithral symphysis, on the pelvic fins, and on the gut above the pelvic fins. Internal pigment is present on the peritoneum above the air bladder and the gut. Opposing streaks of pigment are present laterally and on the ventral margin of the tail on about myomeres 20 to 23. A melanophore is present under the notochord near its tip.

Flexion larvae (Fig. 35B) add pigment near and posteriad to the cleithral symphysis and on the nape. The lateral pigment on myomeres 20 to 23 spreads dorsally and the posterior pigment spot lies over the developing hypural bones.

Postflexion larvae fairly rapidly add pigment over the entire body. Pigment develops soon over the midbrain. By 6.8 mm it has spread over the top of the head and appeared on the cheeks (Fig. 35D). Pigment on the upper and lower jaws is the last to form on the head but develops by 10.7 mm (Fig. 36A). Pigment covers the abdomen on a 5.5-mm specimen and soon spreads over the remainder of the trunk. Lateral pigment on the tail spreads dorsally and ventrally to become a vertical band by 6.8 mm (Fig. 35D). A dorsal patch develops below rays 8 to 10 of the second dorsal fin, and by 7.9 mm, a corresponding lateral patch has formed. By 10.7 mm pigment covers most of the body but is sparse ventrally above the anal fin and at the base of the caudal fin (Fig. 36A). Early juveniles develop a banded pattern against the pigmented body (Fig. 36B and C). Occasion-

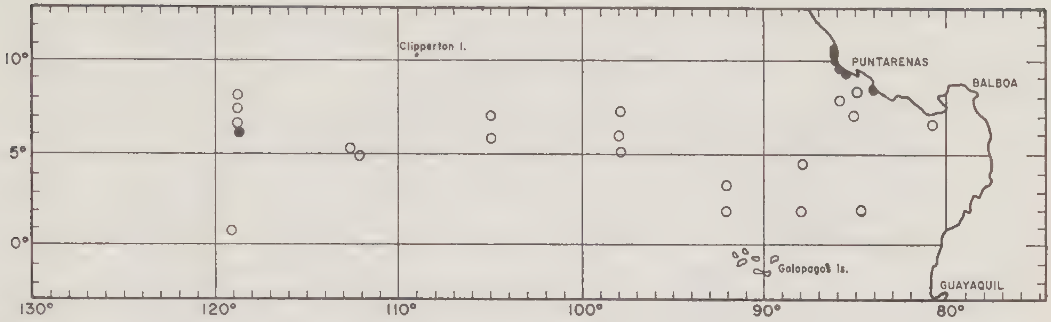

Figure 38. Occurrences of *Psenes cyanophrys* larvae (open circles) and juveniles (closed circles) in the eastern tropical Pacific.

ally, the body is less densely pigmented between the patches until a somewhat larger size, as for example on an 11.7-mm specimen from the Atlantic (Fig. 37).

Psenes maculatus
Lütken, 1880
Figures 39 and 40

Literature.—Reported here from the eastern Pacific for the first time, *P. maculatus* was recorded by Kobayashi (1961) from the western North Pacific at 43°44′N, 154°58′E. His 49.9-mm specimen had 34 vertebrae (from radiograph, Plate 1, Fig. 2). According to Kobayashi (1961), the teeth on his 49.9-mm specimen were arranged in an irregular line on the upper jaw and were sharper and longer than those on the lower jaw. However, Haedrich and Horn (1972) include *P. maculatus* among the species of *Psenes* with "teeth in lower jaw long, knife-like, compressed, close-set, very different from those in the upper jaw;" as pointed out later, our observations reinforce those of Haedrich and Horn.

Material.—We examined one specimen from CalCOFI station 7210-23.143, and a moderate number of collections from the western North Atlantic. The Atlantic material, labelled in Tables 42 and 43 as 0573101-N9 to 0573316-N9, was taken off Charleston, South Carolina, in replicate neuston net hauls at 32°05.0′ to 32°08.5′N and 79°13.0′ to 79°13.5′W on July 14 and 15, 1973.

Table 41. Meristics of cleared and stained larvae and juveniles of *Psenes cyanophrys* (Note: 3.6-mm specimen is a preflexion larva; no flexion larvae available for staining)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 47.297	3.6 NL	II	-	-	LP	I,5	-	2+ 0= 2†	0+4	-	-	-
"	4.7 SL	IX	I,24	II,25	14	I,5	1-9+8-2	12+19=31	2+4	0+1+8	1	0
ETP 30.043	6.9	IX	I,25	III,25	18	I,5	6-9+8-5	12+19=31	2+4	3+1+10	2	3
ETP 14.209	9.7	IX	I,26	III,26	19	I,5	8-9+8-8	12+19=31	2+4	4+1+15	6	6
T.C. 32.023	10.0*	X	I,25	III,25	20	I,5	8-9+8-8	12+19=31	2+4	6+1+13	6	5
T.C. 32.034	12.5*	X	I,25	III,25	20	I,5	8-9+8-8	12+19=31	2+4	6+1+15	9	8
"	14.7*	X	I,25	III,26	19	I,5	8-9+8-8	12+19=31	2+4	6+1+15	9	8
"	15.0*	X	I,24	III,25	19	I,5	9-9+8-7	12+19=31	2+4	6+1+14	11	7
"	16.7*	X	I,25	III,24	19	I,5	8-9+8-7	12+19=31	2+4	6+1+16	11	10
Jord. 57.113	17.5*	IX	I,25	III,25	19	I,5	9-9+8-7	12+19=31	2+4	5+1+16	11	7
T.C. 32.034	18.0*	X	I,25	III,27	19	I,5	8-9+8-7	12+19=31	2+4	6+1+16	11	6
Hunter & Mitchell (V.14.66)	18.9*	X	I,25	III,25	20	I,5	8-9+8-8	12+19=31	2+4	6+1+16	9	8
"	20.4*	X	I,23	III,24	19	I,5	8-9+8-8	12+19=31	2+4	6+1+16	9	8
"	26.4*	X	I,23	III,23	19	I,5	8-9+8-8	12+19=31	2+4	6+1+16	10	7

* Juvenile

† Vertebrae not completely developed

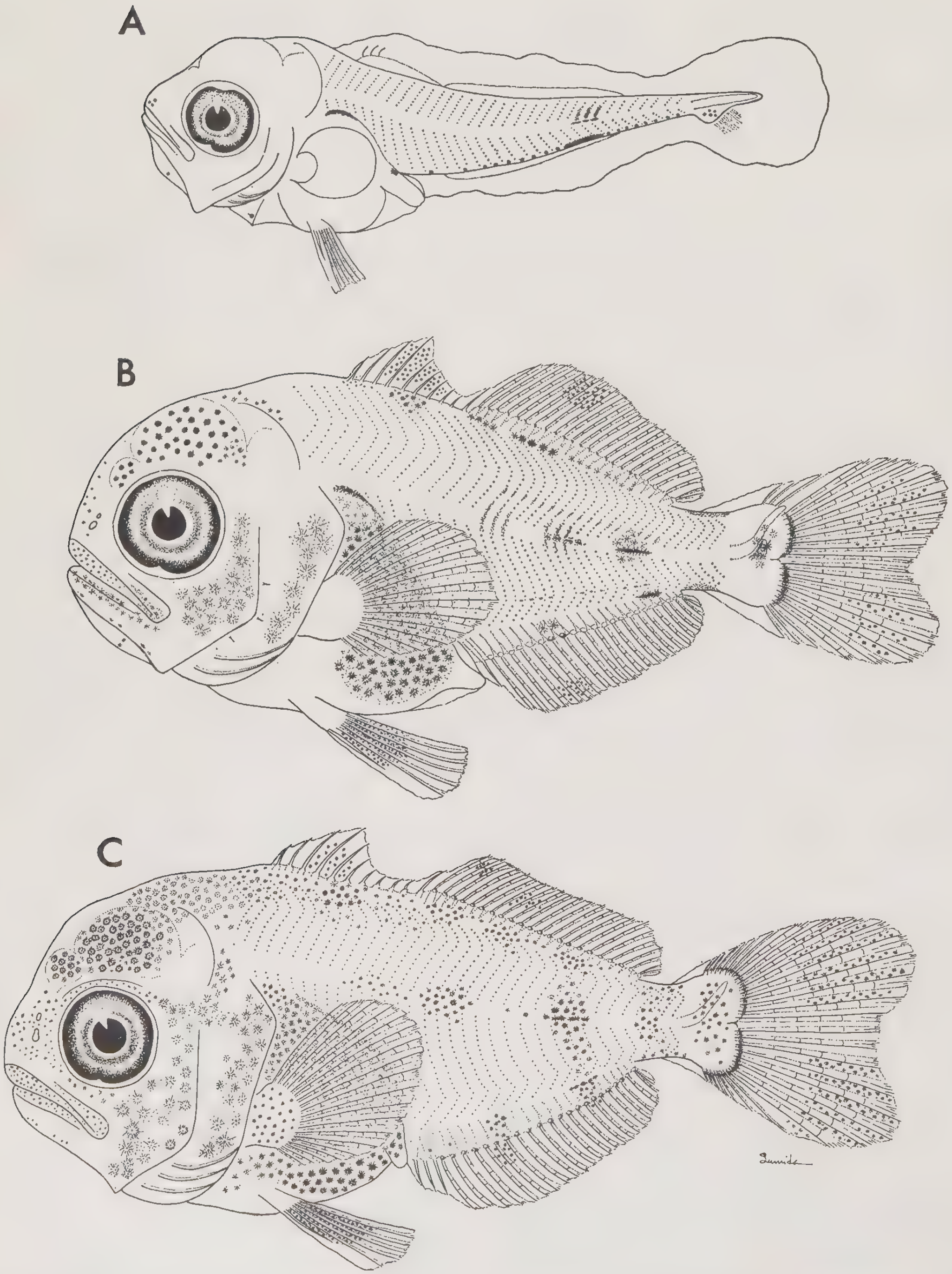

Figure 39. Developmental stages of *Psenes maculatus* (Nomeidae). A—3.8-mm early flexion larva, Atlantic specimen; B—7.6-mm postflexion larva, Atlantic specimen; C—11.6-mm early juvenile, Pacific specimen.

Table 42. Morphometrics, in mm, of larvae and juveniles of *Psenes maculatus* (Atlantic material and one Pacific specimen, 11.6 mm) (specimen above dashed line is a preflexion larva; no flexion larvae available)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
0573236-B505	3.8 NL	1.8	1.1	0.40	0.28	1.2	1.3	-	1.0
0573310-N9	5.8 SL	3.2	2.1	.74	.48	2.7	2.2	3.3	2.2
0573316-N9	6.7	3.7	2.2	.84	.56	3.0	2.4	3.8	2.3
0573311-N9	7.6	4.2	2.6	1.0	.68	3.7	2.5	4.3	2.5
0573310-N9	7.8	4.3	2.6	1.0	.64	3.6	3.0	4.4	2.3
0573315-N9	7.9	4.3	2.8	1.0	.70	3.7	3.2	4.5	2.5
0573316-N9	8.0	4.2	2.7	1.0	.68	3.7	3.1	4.3	2.6
0573315-N9	9.0	5.0	3.2	1.1	.72	4.2	3.3	5.1	3.1
J7210-24.143	11.6*	6.0	4.0	1.4	.96	5.1	4.1	6.1	3.8
0573313-N9	12.4*	6.8	4.6	1.7	1.0	6.4	4.9	7.0	4.2
0573316-N9	12.9*	6.8	4.5	1.8	1.0	6.2	5.0	7.0	4.7
0573313-N9	14.4*	7.5	4.9	2.0	1.1	7.1	5.2	7.7	4.0
0573314-N9	16.5*	9.4	6.0	2.4	1.2	8.4	6.0	9.5	5.3
0573101-N9	22.2*	12.0	7.5	2.9	1.5	11.0	7.7	12.4	7.2
0573314-N9	22.8*	13.0	7.7	3.1	1.7	11.5	8.0	13.4	7.8

* Juvenile

Distribution.—This species is a temperate water form. In the Pacific it is known only from the North Pacific central water mass (Fig. 18).

Distinguishing Characters.—JUVENILES. Early juveniles of *P. maculatus* can be separated by meristics and pigmentation. It is the only *Psenes* with 34 to 35 vertebrae. In several characters early juveniles of *P. maculatus* are more similar to those of *P. arafurensis* than other *Psenes*, but as pointed out earlier, the pigment patterns are distinctively different.

LARVAE.—Larval *P. maculatus* are distinguished by pigmentation and number of myomeres (34 to 35). Preflexion larvae have only two melanophores under the jaw (Fig. 29J) and a line of melanophores on the ventral margin (Fig. 39A). The pigment under the jaw is similar to that on preflexion larvae of *P. cyanophrys*, but the latter lack the line of melanophores on the ventral margin of the body.

Postflexion larvae are easily separated by meristics and pigmentation. Like *P. sio*, *P. maculatus* develops six bands of pigment. Unlike *P. sio*, the fifth band is on the caudal peduncle rather than below the posterior rays of the second dorsal fin and the banded pattern persists to larger sizes in *P. maculatus*.

Meristics.—Vertebrae 12 + 23 = 35; first dorsal X or XI (average 10.9); second dorsal I, 22 or 23 (average I, 22.1); anal III, 21 or 22 (average 21.6); principal caudal rays 9 + 8; secondary caudal rays 8 dorsal + 8 or 9 ventral (average 8.0 + 8.2).

Morphometrics.—The morphometrics of a series from 3.8 to 22.8 mm are given in Table 42. Body proportions of all *Psenes* are discussed in an earlier section (Table 35).

Ossification.—The smallest specimen available for study, a 3.8-mm larva (Fig. 39A), has the pelvic fins fully formed. The anterior three spines of the first dorsal fin and the anlagen of the caudal, second dorsal and anal fins are also developed. By 5.8 mm (Table 43), the first dorsal fin, principal caudal rays, vertebrae, and the branchiostegals are completed. By 7.8 mm, the second dorsal and anal fins have formed their full complement of spines and rays. The pectoral fin has its complete count by

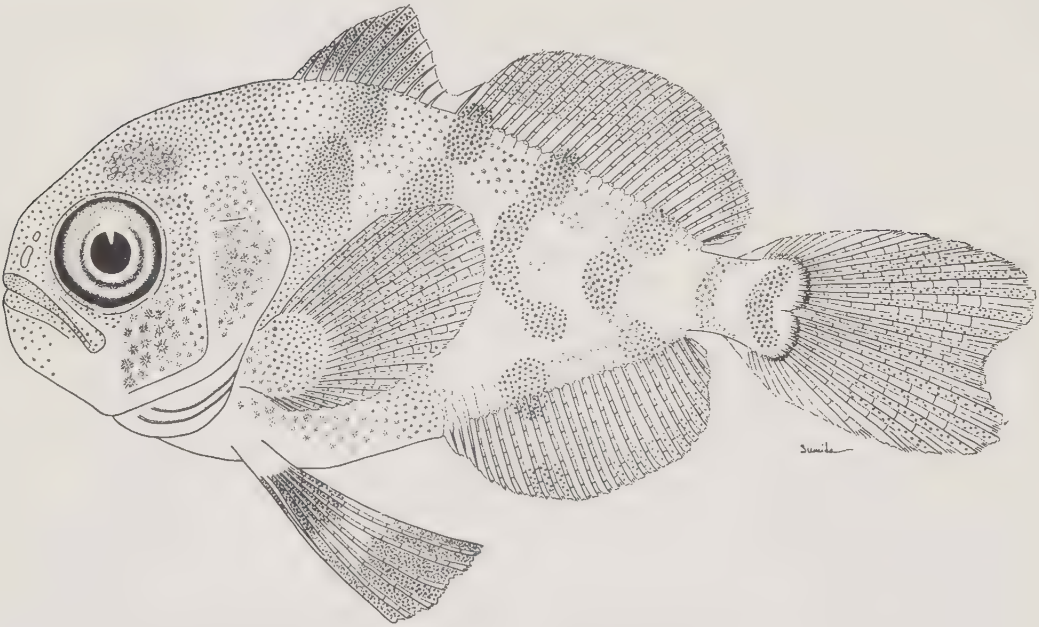

Figure 40. Early juvenile of *Psenes maculatus* (Nomeidae) from the Atlantic, 22.2 mm.

9.0 mm and all secondary caudal rays are present by 12.4 mm.

Weak preopercular spines are present in small specimens (5.0 to 9.0 mm) but become obscured in larger specimens.

Teeth on postflexion larvae are similar in appearance in both jaws. Only the 22.8-mm juvenile has the marked contrast between the teeth in the upper and the lower jaw. On this specimen, the anterior group of five dentary teeth are tapering and sharply pointed as on the premaxillary, but the

Table 43. Meristics of cleared and stained postflexion larvae and juveniles of *Psenes maculatus* (Note: all are Atlantic specimens taken off South Carolina)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
0573310-N9	5.8 SL	X	6	III,8	18	I,5	0-9+8-0	12+23=35	2+4	1+1+9	4	3
0573316-N9	6.7	VIII	-	II,5	18	I,5	2-9+8-3	12+23=35	2+4	2+1+9	6	5
0573310-N9	7.8	XI	I,23	III,22	18	I,5	5-9+8-5	12+23=35	2+4	4+1+9	6	5
0573315-N9	7.9	XI	I,22	III,21	20	I,5	5-9+8-5	12+23=35	2+4	4+1+10	9	5
0573316-N9	8.0	XI	I,22	III,19	19	I,5	4-9+8-4	12+23=35	2+4	3+1+9	7	5
0573315-N9	9.0	XI	I,22	III,22	21	I,5	6-9+8-6	12+23=35	2+4	4+1+12	5	4
0573313-N9	12.4*	X	I,22	III,21	22	I,5	8-9+8-8	12+23=35	2+4	6+1+13	9	8
0573316-N9	12.9*	XI	I,22	III,22	22	I,5	8-9+8-8	12+23=35	2+4	7+1+14	10	8
0573313-N9	14.4*	XI	I,22	III,21	21	I,5	8-9+8-9	12+23=35	2+4	8+1+14	9	6
0573314-N9	16.5*	XI	I,22	III,22	20	I,5	8-9+8-8	12+23=35	2+4	7+1+15	10	8
0573314-N9	22.8*	XI	I,22	III,22	22	I,5	8-9+8-8	12+23=35	2+4	10+1+17	10	11

* Juvenile

posterior group of six dentary teeth are wide and blade-like, similar to those in *Tetragonurus*.

Scales form on the anterior midline of the body by 12.4 mm, on the pectoral base by 14.4 mm, and over the abdomen by 16.5 mm. More than half of the body is scaled on a 22.8-mm specimen. Atlantic specimens of 12.4 mm and larger are considered juveniles because the fins have complete counts and scales are forming; the single specimen from the Pacific, 11.6 mm, has the complete fin count, and is probably a juvenile.

Pigmentation.—Early flexion larvae (3.8 mm) have a series of melanophores on the ventral margin interrupted by a pigment streak at myomeres 23 to 26 (Fig. 39A). Lateral line pigment develops at about myomeres 25 to 27 with pigment spreading dorsally along the myosepta. Pigment is present on the upper jaw, over the developing hypural bones, and on the peritoneum over the air bladder. A single melanophore is present near the cleithral symphysis, and on either side of the isthmus (Fig. 29J).

Postflexion larvae add considerable pigment and soon develop a strong banded pattern. By 7.6 mm, pigment becomes heavy over the head, jaws, operculum and abdomen (Fig. 39B), with some embedded pigment on the body and considerable myoseptal pigment. There are four dorsal pigment patches or rows of melanophores, the first under the first dorsal fin, the second at the origin of the second dorsal fin, and the third and fourth under the second dorsal fin; also two ventral patches, one above anal rays 6 to 8 and the other above rays 17 to 20. Pigment patches are conspicuous at the base of the caudal fin as well as along the lateral line at myomeres 18 to 22 and 26 to 28. By 11.6 mm the banding pattern is evident (Fig. 39C). The pigment bands at the caudal peduncle and under the posterior part of the second dorsal fin have formed. The more anterior bands are represented by patches near the dorsal margin and at the lateral line. The pigment pattern of the 22.2-mm juvenile (Fig. 40) is described in an earlier comparative section on *Psenes* pigmentation.

Psenes pellucidus
Lütken, 1880
Figures 41 to 44

Literature.—Fitch (1948) reported on a 370-mm specimen taken off Newport Beach, California. Fitch used the name *Icticus ischanus* Jordan and Thompson, 1914, which subsequently was synonymized with *Psenes pellucidus* by Haedrich (1967). Fitch and Lavenberg (1968) reported on two juveniles taken off northern Baja California. Horn and Haedrich (1973) gave measurements and counts for the Newport Beach specimen. Abe (1954) reported on a specimen from off Japan under the name *Papyrichthys ischanus*.

Material.—Study material consisted of larvae from seven CalCOFI stations, six EASTROPAC stations, one Shellback station, and of juveniles from six stations on TOWNSEND CROMWELL cruise 51. Several samples also were available from the western North Atlantic.

Distribution.—*P. pellucidus* has a disjunct distribution in the eastern Pacific. Specimens were taken in transition waters of the California Current from Catalina Island south to off Punta Eugenia, Baja California (Fig. 18). In tropical waters it was found offshore between 5°N and 5°S (Fig. 25). This distribution may be explained by a preference for cooler or more productive waters of upwelling regions or by an exclusion from oxygen minimum areas of the eastern Pacific. Although the distributions of *P. pellucidus* and *P. sio* are almost disjunct, they are more complex than was known to Horn and Haedrich (1973) who speculated that they "are closely related species which replace one another north to south in the eastern Pacific."

Distinguishing Characters.—JUVENILES. *Psenes pellucidus* is distinguished by its soft, flexible compressed body and by the high vertebral and fin ray counts (Table 1). Only *Nomeus* has as high a vertebral count, but it has somewhat lower second dorsal and anal fin ray counts and strikingly different pigment patterns.

LARVAE. Preflexion larvae resemble *P.*

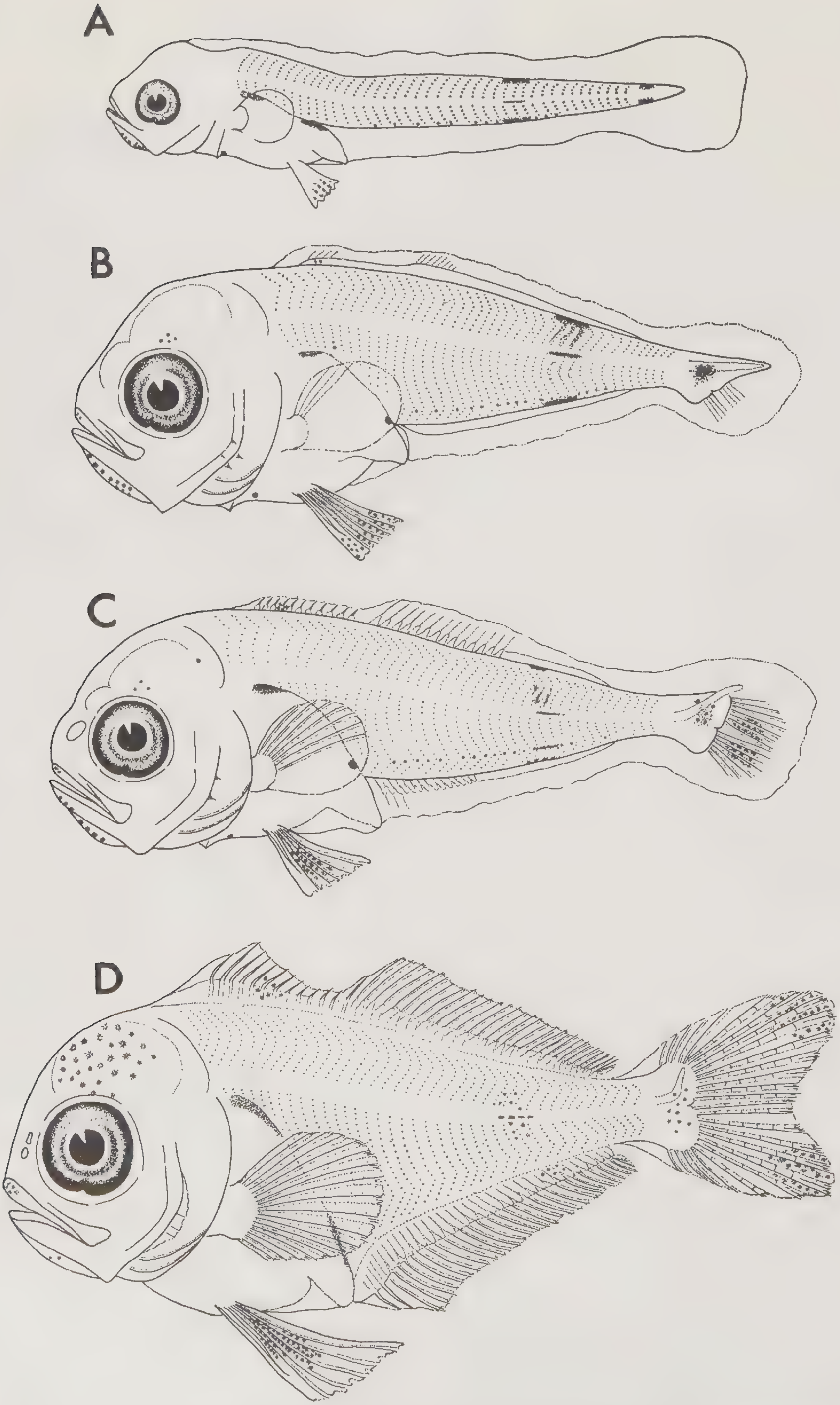

Figure 41. Developmental stages of *Psenes pellucidus* (Nomeidae). A—3.8-mm preflexion larva; B—5.2-mm early flexion larva; C—5.9-mm flexion larva; D—9.7-mm postflexion larva.

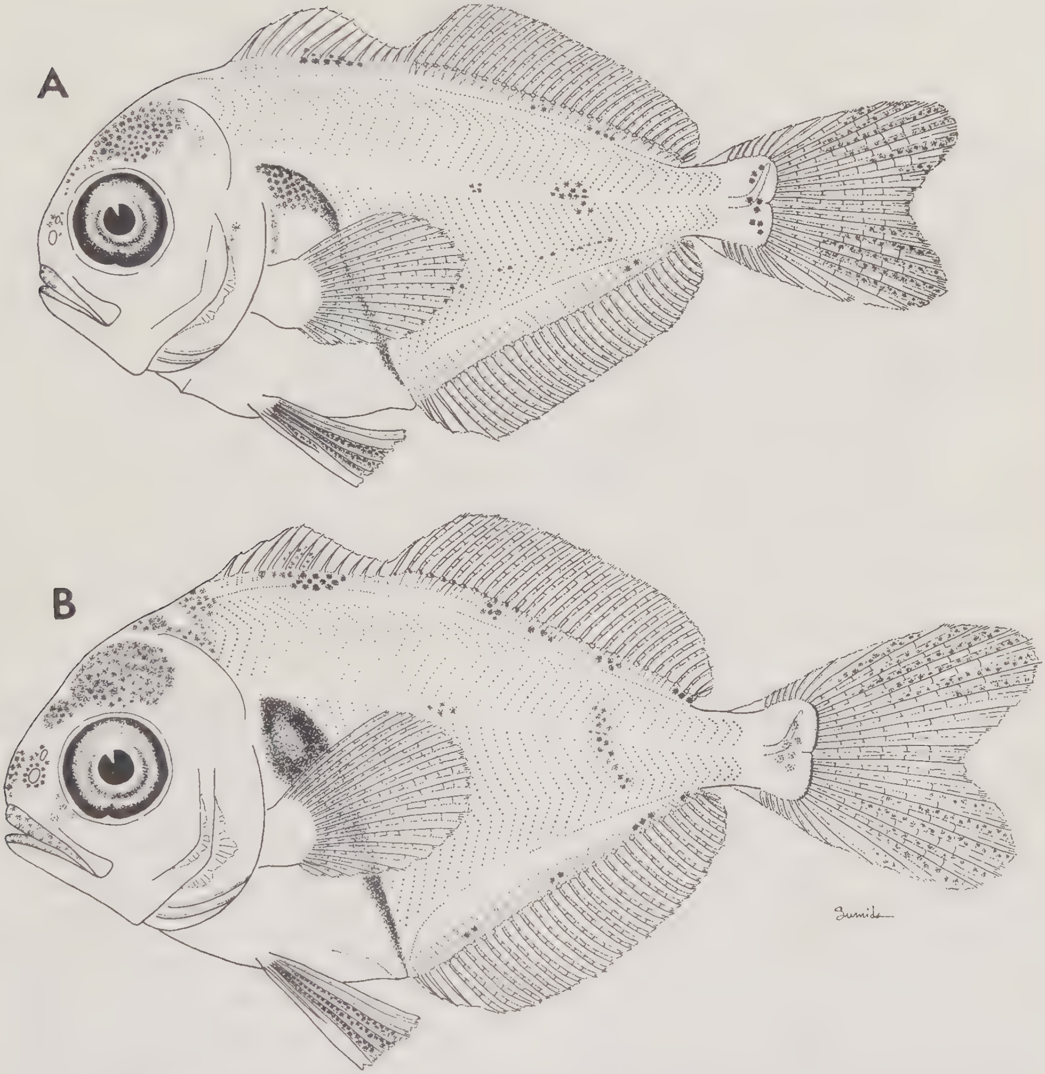

Figure 42. Developmental stages of *Psenes pellucidus* (Nomeidae). A—12.4-mm postflexion larva; B—13.4-mm early juvenile.

sio. Both have pigment under the lower jaw (Fig. 29) and ventral pigment spots on the tail portion of the body. However, *P. pellucidus* has more myomeres (40 to 42 vs. 36 to 38), lacks the dorsal pigment spot at myomeres 12 to 13, and develops lateral pigment more posteriad at myomeres 27 to 30 rather than at 22 to 25 as in *P. sio*.

Meristics.—Vertebrae 13 + 27 to 29 = 40 to 42 (average 41.1) (rarely 14 + 27 = 41); first dorsal XI or XII (average 11.9); second dorsal I (26) 28 to 30 (average I, 28.6); anal III, 27 to 30 (average III, 28.7); principal caudal rays 9 + 8; secondary caudal rays 8 to 10 dorsal + 8 to 10 ventral (average 8.9 + 8.9).

Table 44. Meristics of 21 juveniles of *Psenes pellucidus* available from the eastern Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Catalina Isl.				64.5	13+28=41	XII	I,26	III,27	9-17-9
B6509-113.40	29°02'N	115°57'W	IX.15.65	16.0	13+28=41	XII	I,28	III,28	-
"	"	"	"	19.3	13+28=41	XII	I,28	III,28	9-17-9
"	"	"	"	21.0	13+28=41	XII	I,28	III,29	9-17-9
"	"	"	"	27.0	13+28=41	XII	I,28	III,27	9-17-9
T.C. 51.078	02°54'N	121°54'W	XI.17.70	60.0	14+27=41	XII	I,29	III,27	10-17-9
T.C. 51.082	01°56'N	121°41'W	XI.18.70	21.0	13+28=41	XI	I,29	III,28	8-17-9
"	"	"	"	23.0	13+29=42	XII	I,29	III,30	8-17-9
"	"	"	"	24.4	13+28=41	XII	I,29	III,28	9-17-9
"	"	"	"	25.0	13+28=41	XII	I,28	III,30	9-17-9
"	"	"	"	26.0	13+29=42	XII	I,30	III,30	9-17-9
"	"	"	"	32.0	13+28=41	XII	I,30	III,29	9-17-9
"	"	"	"	35.0	13+29=42	XII	I,29	III,30	9-17-9
"	"	"	"	95.0	13+27=40	XII	I,28	III,30	9-17-9
T.C. 51.086	01°52'N	120°05'W	XI.19.70	23.0	13+28=41	XI	I,28	III,29	8-17-8
T.C. 51.070	03°02'S	121°00'W	XI.13.70	35.0	13+28=41	XII	I,29	III,29	?-17-9
"	"	"	"	35.5	13+28=41	XII	I,28	III,29	10-17-9
T.C. 51.063	03°44'S	119°30'W	XI.12.70	39.0	13+29=42	XII	I,30	III,30	10-17-10
"	"	"	"	54.0	13+28=41	XII	I,29	-	9-17-9
T.C. 51.048	04°02'S	118°48'W	XI.8.70	21.0	13+28=41	XII	I,28	III,28	8-17-8
"	"	"	"	33.0	13+28=41	XII	I,29	III,29	8-17-8

Meristics of 21 specimens from about 4°S to about 29°N and from about 115°W to about 122°W are given in Table 44. No geographical variation in any count is indicated.

Morphometrics.—Morphometrics of a developmental series is presented in Table 45. Body proportions are discussed for all *Psenes* in an earlier section (Table 35).

Ossification.—Only five specimens were cleared and stained because of a limited amount of available material. Therefore, a detailed account of the ossification pattern in *P. pellucidus* is not presented, and fin formation is based on careful examination of remaining unstained specimens in the collection.

The pelvic fins are present on the smallest available perflexion larva of 3.8 mm (Fig. 41A). On a 5.2-mm early flexion larva, four spines are developing anteriorly in the first dorsal fin and rays are beginning to form in the second dorsal and pectoral fins; the anlagen of the caudal and anal fins are evident (Fig. 41B) and on a 5.9-mm late flexion specimen, the latter fins have rays and spines differentiated (Fig. 41C). There is a size gap between the 5.9-mm and 9.7-mm specimens available from the Pacific. In the latter specimen, the first dorsal, second dorsal, and pectoral fins have their full count of spines and/or rays; the anal fin has only two spines, whereas larger specimens all have three anal spines (Figs. 42 and 43). The caudal fin has 4 + 4 secondary rays as well as 9 + 8 principal rays. However, a 7.4-mm specimen from the Atlantic has but one anal spine (Fig. 44B), suggesting a gradual acquisition of the full complement of three anal spines. A 12.0-mm specimen has the complete number of 8 + 8 secondary caudal rays developed (Table 46).

A total of 40 vertebrae (13 + 27), which is a low but complete number for the species, is ossifying in a 12.0-mm specimen. The complete number of 2 + 4 branchiostegal rays is evident by 5.2 mm along with a few gill rakers on the first arch. The full count of gill rakers is still not achieved at 27.0 mm. Small preopercular spines are formed by 5.2 mm and become embedded by 9.7 mm.

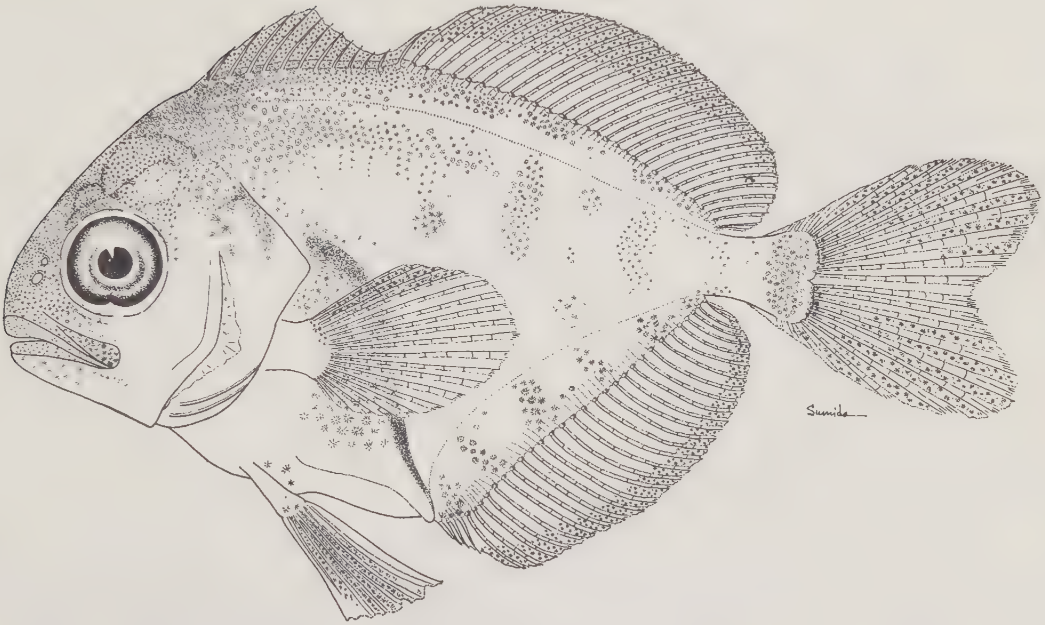

Figure 43. Early juvenile of *Psenes pellucidus* (Nomeidae), 24.4 mm.

These weak spines are finally resorbed at about 18.0 mm.

Premaxillary and dentary teeth appear from ca. 5.5 mm, and gradually increase in number with size (Table 46).

Scales are not evident on a 12.0-mm or 17.9-mm cleared and stained specimen. However, a 20.8-mm specimen is scaled in the area of the pectoral and pelvic girdle, and a 27.0-mm specimen is scaled over most of the body. The latter two specimens have the adult number of secondary caudal rays. From the above, it is difficult to pinpoint when the larval period ends and when the juvenile period begins. Fin formation appears to be complete by 13.4 mm but scale formation was first observed on a 20.8-mm specimen. We are inclined to accept the completion of fin formation as the end of the larval period.

Pigmentation.—Pigmentation on larvae of *P. pellucidus* most closely resembles the patterns on larvae of *P. sio*. Both species have pigment under the lower jaw on preflexion and flexion stage larvae (Fig. 29), a series of ventral margin spots posterior to the anus, opposing dorsal, ventral, and lateral line pigment streaks on the tail portion of the body, and pairs of dorsal and ventral spots near the tip of the notochord.

On preflexion larvae ca. 3.8 mm (Fig. 41A), pigment under the lower jaw is in the form of an inverted "Y," but melanophores are more scattered and dense compared to those in *P. sio*. A pigment spot is developed near the cleithral symphysis. Pigment is present on the precociously forming pelvic fins and internally on the peritoneum. Tail pigment consists of a series of ventral margin spots (13 on specimen illustrated), opposing dorsal, ventral, and lateral line blotches of pigment at myomeres 27 to 30, and opposing dorsal and ventral spots near the tip of the notochord.

During flexion, at 5.2 to 5.9 mm, a few pigment spots develop on the upper jaw and on the head above the eyes (Fig. 41B and C). Pigment at the tip of the notochord now

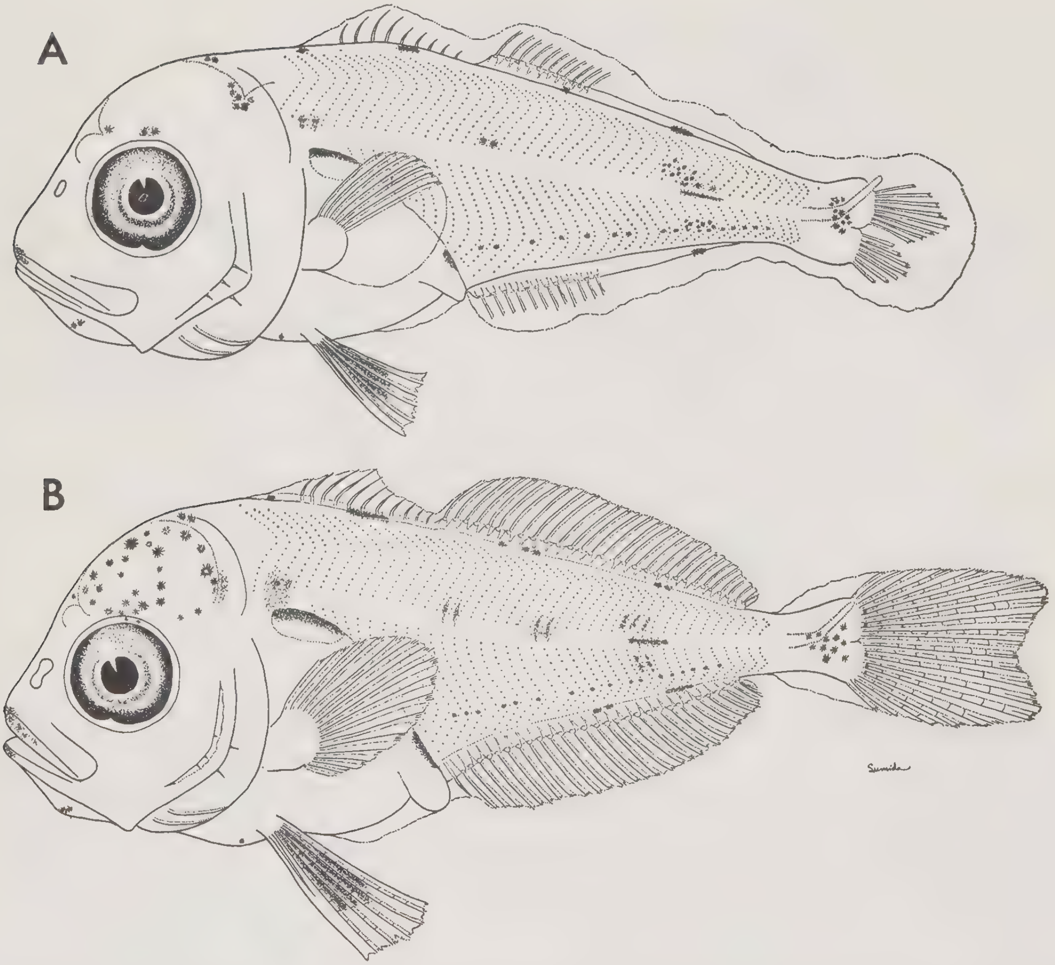

Figure 44. Developmental stages of *Psenes pellucidus* (Nomeidae) from the Atlantic. A—5.9-mm late flexion larva; B—7.4-mm postflexion larva.

forms a patch over the hypural bones. The developing principal caudal rays also become pigmented on what will be the two lobes of the caudal fin. A few melanophores form near the anterior base of the first dorsal fin. The opposing dorsal, ventral, and lateral line tail pigment is at myomeres 28 to 31; the ventral margin spots on the tail number 17 or 18.

Pigment is added gradually in postflexion larvae. The 9.7-mm specimen (Fig. 41D) has added more pigment to the top of the head, has reduced the pigment under the lower jaw, and lost the ventral margin series on the tail. The series of ventral pigment spots are still persistent in a 12.4-mm specimen (Fig. 42A), however, although now internal and displaced dorsad. On both specimens the anterior dorsal pigment patch has spread out between the bases of the middle spines of the first dorsal fin. Pigment is added in small patches on the body adjacent to the second dorsal and anal fins; the 13.4-mm specimen (Fig. 42B) has an an-

Table 45. Morphometrics, in mm, of larvae and juveniles of *Psenes pellucidus* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
B5908-113.45	3.8 NL	1.7	0.90	0.33	0.20	0.76	-	-	1.4
B5908-110.55	4.6	1.8	1.1	0.44	0.28	1.1	-	-	1.5
ETP 11.098	5.2	2.4	1.5	0.56	0.38	1.7	1.8	2.6	1.6
S.B. 178	5.9	2.8	1.7	0.64	0.40	1.9	1.8	2.9	2.0
ETP 50.090	9.7 SL	4.7	3.1	1.2	0.56	4.2	3.1	5.0	2.8
T.C. 51.063	12.4	6.1	3.5	1.4	0.72	6.2	3.6	6.2	4.1
T.C. 51.048	13.4*	6.2	3.6	1.6	0.72	6.7	3.9	6.5	4.1
ETP 12.224	17.0*	8.7	4.8	2.0	1.2	8.5	5.8	8.8	5.7
B6509-113.40	18.2*	8.4	5.3	2.1	1.2	8.8	5.3	8.8	5.2
T.C. 51.082	21.2*	11.2	6.8	2.4	1.5	10.9	6.4	11.7	7.4
"	24.4*	12.2	7.7	2.7	1.8	13.5	6.5	12.7	7.7
B6509-113.40	26.7*	13.2	8.8	3.1	2.0	15.2	7.4	13.7	8.4

* Juvenile

terior lateral line patch at myomeres 18 to 20. Early juveniles of *P. pellucidus* (Fig. 43) are only moderately pigmented compared to other species of *Psenes*. The caudal, first dorsal, and pelvic fins are rather heavily pigmented, whereas the second dorsal and anal fins are pigmented on their outer margin and the pectoral fin only between its upper rays. Pigment on the body is patchy, with several bands of pigment incompletely developed on the tail portion of the body.

Several specimens from the Atlantic develop more pigment on the body and at smaller sizes than the Pacific material (Fig. 44). Lateral pigment forms on myomeres 2 and 3, 16 and 17, 29 to 32, and over the caudal peduncle on a 5.9-mm larva (Fig. 44A). Pigment patches along the dorsal margin of the body also form early. A 7.4-mm larva (Fig. 44B) has additional lateral pigment on myomeres 23 and 24. No specimens larger than 7.4 mm were available for study from the Atlantic.

Psenes sio Haedrich, 1970

Figures 45 to 47

Literature.—Haedrich (1970) described *Psenes sio* from five specimens collected on Step 1 Expedition of Scripps Institution of Oceanography between 1°24′ to 11°10′S and 80°01′ to 95°04′W. A larger specimen, 219 mm, collected at 22°N, 108° W was reported by Horn and Haedrich (1973).

Table 46. Meristics of cleared and stained larvae and juveniles of *Psenes pellucidus* (specimen above dashed line is undergoing notochord flexion; no preflexion larvae available for staining)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchiostegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP 60.093	5.5 NL	XI	I,19	II,17	12	I,5	1-9+8-1	13+19=32†	2+4	0+1+6	1	0
ETP 12.094	12.0 SL	XII	I,28	II,30	18	I,5	8-9+8-8	13+27=40	2+4	6+1+13	6	12
B6509-113.40	17.9*	XII	I,28	III,28	19	I,5	8-9+8-8	13+28=41	2+4	7+1+12	8	10
"	20.8*	XII	I,28	III,28	19	I,5	9-9+8-9	13+28=41	2+4	7+1+13	12	11
"	27.0*	XII	I,28	III,27	20	I,5	9-9+8-9	13+28=41	2+4	7+1+13	13	16

* Juvenile

† Vertebrae not completely developed

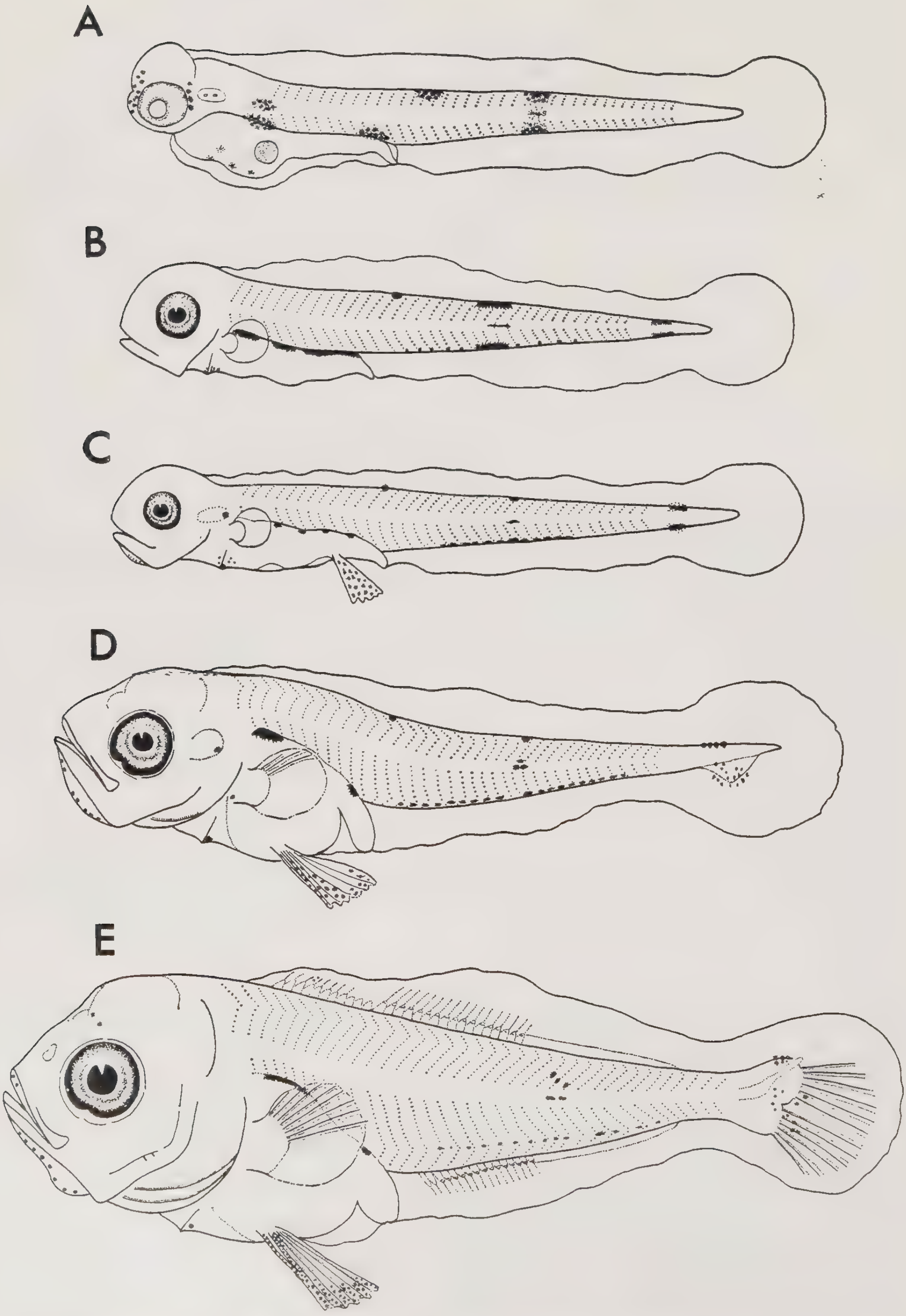

Figure 45. Developmental stages of *Psenes sio* (Nomeidae). A—2.4-mm late yolk-sac larva; B—2.1-mm preflexion larva; C—3.5-mm preflexion larva; D—4.3-mm preflexion larva; E—5.6-mm late flexion larva.

Table 47. Meristics of 25 juveniles of *Psenes sio* selected from over its distributional range in the eastern Pacific (counts made from radiographs)

Station	Location		Date	Size-SL (mm)	Vertebrae	1st Dorsal fin	2nd Dorsal fin	Anal fin	Caudal fin
	Lat.	Long.							
Sailfish Stomach	23°40'N	109°45'W	VI.23.57	30.0	12+25=37	XI	I,23	II,23	7-17-8
J7205-157G115	23°26'N	107°45.2'W	VI.7.72	15.4	12+24=36	XI	I,23	II,23	9-17-9
Striped Marlin Stom.	23°20'N	109°21'W	VI.23.57	22.7	12+25=37	XI	I,22	II,23	8-17-8
J7205-157G100	23°17'N	107°58'W	VI.7.72	12.4	12+24=36	XI	I,22	II,23	8-17-7
ETP 50.252	14°48'N	98°10'W	XI.27.67	14.8	12+25=37	XII	I,24	II,24	9-17-9
Jord. 57.014	13°36'N	118°53'W	XI.9.70	24.6	12+25=37	XI	I,23	II,24	8-17-8
Jord. 57.013	13°27'N	119°01'W	XI.9.70	35.0	12+24=36	XI	I,23	II,23	9-17-9
"	"	"	"	65.0	12+25=37	XI	I,24	II,24	9-17-10
"	"	"	"	48.0	12+25=37	XI	I,22	II,23	8-17-9
Jord. 57.012	13°16'N	119°23'W	XI.8.70	29.5	12+24=36	XI	I,23	II,23	8-17-9
"	"	"	"	21.6	12+25=37	XI	I,24	II,25	8-17-9
Jord. 57.019	12°32'N	118°54'W	XI.10.70	18.6	12+25=37	XI	I,24	II,24	8-17-8
Jord. 57.053	09°51.4'N	117°32.5'W	XI.16.70	24.6	12+25=37	XI	I,24	II,24	9-17-8
ETP 13.328	09°42'N	95°03'W	III.18.67	16.2	12+25=37	XI	I,25	II,24	8-17-8
ETP 50.234	08°47'N	98°05'W	XI.24.67	15.0	12+24=36	XII	I,23	II,23	9-17-8
Jord. 65.037	00°12'S	98°02'W	VIII.25.71	44.0	12+25=37	XI	I,26	II,24	9-17-9
Jord. 65.208	00°30'S	96°13'W	IX.27.71	61.9	12+26=38	XII	I,24	II,25	10-17-10
Jord. 65.214	00°30'S	97°13'W	IX.28.71	27.1	12+26=38	XI	I,25	II,25	9-17-9
Jord. 65.142	03°29.4'S	96°24.3'W	IX.8.71	39.9	12+25=37	XI	I,23	II,24	8-17-8
Jord. 65.150	03°57'S	97°40'W	IX.9.71	30.0	12+26=38	XI	I,25	II,26	9-17-9
Jord. 65.144	04°00.5'S	97°02'W	IX.8.71	34.5	12+26=38	XII	I,23	II,25	8-17-8
"	"	"	"	33.5	12+26=38	XII	I,24	II,25	8-17-8
Jord. 65.138	04°05.2'S	96°31'W	IX.7.71	20.5	12+26=38	XI	I,24	II,24	8-17-8
"	"	"	"	29.5	12+24=36	XI	I,23	II,23	9-17-9
South Tow Exp.	23°24.5'S	72°20.1'W	IV.29.72	54.6	13+25=38	XII	I,24	II,25	9-17-?

Material.—Over 100 collections of larvae were examined from EASTROPAC and CalCOFI cruises. Approximately 20 collections of juveniles were examined from later cruises in the eastern tropical Pacific made during 1970 and 1971.

Distribution.—*Psenes sio* is common nearshore in the eastern Pacific (Fig. 48) and in the Gulf of California (Fig. 49). It extends offshore south of the equator to almost 100° W; north of 9°N it is found out to 120°W. This species, which is endemic to the eastern Pacific, appears to be well adapted to waters with a marked oxygen minimum layer.

Distinguishing Characters.—JUVENILES. Juveniles of *P. sio* are distinguished by meristics, pigmentation and morphometrics. The total vertebral count of 36 to 38 is unique among nomeids. It is the only *Psenes* with two anal spines. Early juveniles of *P. sio* are less deep-bodied than other *Psenes* and become uniformly pigmented at a smaller size (25 to 30 mm).

LARVAE. Larvae of *P. sio* are distinguished by a combination of pigmentation, meristics including myomere counts, and morphometrics, especially body depth. Preflexion larvae are rather similar to those of *P. pellucidus* from the eastern Pacific. Both have heavy pigment under the lower jaw (Fig. 29), and a line of ventral pigment spots on the tail. However, preflexion larvae of *P. sio* have pigment on the dorsal body margin at myomeres 12 and 13 which is lacking in *P. pellucidus*. Also the conspicuous dorsal, lateral and ventral pigment patches on the tail develop on myomeres 22 to 25 in *P. sio* but on myomeres 27 to 29 in *P. pellucidus*. *P. sio* has several fewer myomeres (36 to 38 vs. 40 to 42) than *P. pellucidus* and is less deep-bodied.

Meristics.—Vertebrae 12 + 24 to 26 = 36 to 38 (average 37.0) (rarely 13 + 25 = 38); first dorsal XI or XII (average 11.3); second dorsal I, 22 to 26 (average 23.6); anal II, 23 to 26 (average II, 23.9); principal caudal rays 9 + 8; secondary caudal rays 7

Table 48. Morphometrics, in mm, of larvae and juveniles of *Psenes sio* (specimens between dashed lines are undergoing notochord flexion)

Station	Body length	Snout to anus	Head length	Eye diameter	Snout length	Body depth at pectoral fin base	Snout to origin dorsal fin	Snout to origin anal fin	Snout to origin pelvic fin
ETP 46.124	2.1 NL	0.98	0.42	0.17	0.10	0.42	-	-	-
S5706-153.25	3.2	1.6	0.72	0.31	0.16	0.80	-	-	1.2
S5706-157.25	3.6	1.5	0.80	0.30	0.20	0.72	-	-	1.1
S5706-153.20	4.9	2.1	1.5	0.49	0.35	1.5	1.7	2.3	1.4
ETP 13.019	4.2	2.2	1.5	0.58	0.28	1.8	1.6	2.3	1.5
	4.7	2.4	1.5	0.56	0.37	1.5	1.6	2.4	1.6
Step 1-40	5.5	2.8	1.8	0.72	0.44	2.1	2.1	2.9	1.6
	6.0 SL	3.0	1.8	0.70	0.48	2.2	1.9	3.1	1.8
ETP 60.189	7.2	3.7	2.5	0.86	0.54	3.1	2.7	3.9	2.4
S.B. 115	8.1	4.0	2.5	1.0	0.59	3.0	2.6	4.2	2.4
ETP 14.001	9.1	4.6	2.8	1.1	0.68	3.7	3.2	4.7	3.1
ETP OP-044	11.0	5.8	3.4	1.4	0.92	4.4	3.3	6.0	3.2
"	12.5	6.5	3.6	1.5	0.83	4.9	3.9	6.7	3.8
ETP 47.246	13.5	6.8	4.4	1.7	1.0	6.1	4.8	7.2	4.2
Baitwell-Peru	14.4*	7.1	4.6	1.9	1.2	6.0	4.8	7.5	4.6
ETP 50.234	15.0*	7.6	4.5	1.7	1.0	6.4	4.8	7.9	4.6
ETP 47.246	15.9*	8.3	5.2	1.7	1.5	6.5	5.3	8.6	5.4
ETP 12.026	22.1*	11.2	7.1	2.3	1.6	9.4	6.7	11.9	7.5

* Juvenile

to 10 dorsal + 8 to 10 ventral (average 8.5 + 8.6).

Meristics of 25 specimens from about 23°S to about 24°N and from about 72°W to about 119°W are given in Table 47. No geographical variation of any count is indicated.

Morphometrics.—Morphometrics of a series of 18 specimens are presented in Table 48. Body proportions are discussed in an earlier section for all *Psenes* (Table 35).

Ossification.—As in all *Psenes* larvae, the pelvic fins are the first to form rays. A preflexion larva (3.4 mm) has the complete pelvic fin complement of one spine and five rays (Table 49). During notochord flexion rays begin to form in the caudal and pectoral fins, and spines begin to form in the first dorsal. In the caudal fin, rays first form at the junction of the two lobes; in the pectoral fins, rays ossify ventrad from the dorsal margin. In the dorsal fin, spines first develop anteriad at the origin and rapidly develop posteriad. The full complement of dorsal spines is developed before flexion is complete (4.7 mm). The second dorsal and anal fins begin forming at the same size and are complete by the end of flexion, at 6.1 mm. Only the secondary caudal rays form gradually; 8 + 8 rays are present on a 12.4-mm specimen and 9 + 9 rays are present on a 14.4-mm specimen. The full complement is 7 to 10 + 8 to 10 rays.

The axial skeleton begins ossification at the same time that the caudal begins forming. On the 4.3-mm and 4.6-mm specimens, only the four anterior neural spines are ossifying. On a 5.4-mm specimen, all the precaudal vertebrae are formed and neural spines are ossifying on vertebrae 13 to 27, haemal spines on vertebrae 13 to 24, but centra are ossifying only on vertebrae 13 to 19. By 6.1 mm all centra, neural, and haemal spines are ossifying. The separation into precaudal and caudal vertebrae can readily be made in the 5.4- to 6.1-mm specimens, inasmuch as the haemal spines are well formed on the 13th and following vertebrae, but ribs are not yet formed on the vertebral column.

The terminal centrum, which is designated simply as a "ural" centrum, is long and markedly tapered. It is several times as long

Table 49. Meristics of cleared and stained larvae and juveniles of *Psenes sio* (specimens between dashed lines are undergoing notochord flexion)

Station	Size (mm)	1st Dorsal fin	2nd Dorsal fin	Anal fin	Pect. fin (left)	Pelvic fins	Caudal fin	Vertebrae	Branchio-stegal rays	Gill rakers (right)	Teeth (left)	
											Prem.	Dent.
ETP OP-044	3.4 NL	-	-	-	-	I,5	-	-	0+4	-	-	-
S.B. 155	4.3	IV	-	-	3	I,5	0-3+3-0	4+ 0= 4†	2+4	-	-	-
S.B. 154	4.6	II	-	-	2	I,5	0-2+2-0	4+ 0= 4†	2+4	-	-	-
S.B. 155	4.7	XII	I,11	I,10	9	I,5	0-7+8-0	12+12=24†	2+4	0+1+4	-	-
S.B. 154	5.2	XI	I,15	II,13	8	I,5	0-7+8-0	12+15=27†	2+4	0+1+4	-	-
B6001-157.25	6.1 SL	XII	I,22	II,23	16	I,5	3-9+8-3	12+24=36	2+4	1+1+8	3	2
ETP 50.238	6.2	XI	I,23	I,25	16	I,5	3-9+8-3	12+25=37	2+4	0+1+8	3	1
ETP 60.189	7.8	XII	I,24	II,23	17	I,5	6-9+8-6	12+24=36	2+4	3+1+8	3	2
S.B. 150	8.3	XI	I,25	II,24	16	I,5	4-9+8-4	12+25=37	2+4	2+1+10	3	1
ETP 60.276	9.0	XI	I,24	II,23	18	I,5	6-9+8-6	12+25=37	2+4	3+1+9	5	4
ETP 47.246	12.4	XI	I,24	II,24	17	I,5	8-9+8-8	12+24=36	2+4	4+1+9	6	5
ETP 50.238	13.4	XI	I,24	II,24	16	I,5	8-9+8-8	12+25=37	2+4	3+1+11	6	7
Baitwell-Peru	14.4*	XII	I,22	II,24	17	I,5	9-9+8-9	12+26=38	2+4	5+1+11	6	7
9°27'N 89°18'W	22.5*	XII	I,24	II,23	18	I,5	10-9+8-10	13+25=38	2+4	8+1+13	10	15

* Juvenile

† Vertebrae not completely developed

as any other centrum, and on some specimens is slightly expanded at its junction with the superior hypurals. Although the ural centrum ossifies as a unit, and hence furnishes no evidence of past fusions, both its length and its appearance give the impression of a fused bone made of at least two parts, one part supporting the superior hypurals, the other the inferior hypurals. This impression is further enhanced by the fact that the stegural (anterior pair of the uroneurals) forms on the posterior half of the ural centrum, opposite the superior hypurals. The hypurals are comprised of two superior and two inferior bones (including the parhypural). At first formation, there are six centers of ossification of hypurals, but fusion soon occurs between the two inferior hypurals adjacent to the parhypural. Fusion occurs less rapidly between the inner two superior hypurals, which on many postflexion larvae are united only at their distal margins. The three epurals and the second pair of uroneurals are the last of the ural bones to ossify. The vertebra immediately anterior to the ural centrum lacks a neural spine but has a specialized neural arch and an autogenous haemal spine. The haemal spine is also autogenous on the second vertebra anterior to the ural, but the neural spine is well-developed and spatulate. Occasionally, the haemal spine of the third vertebra anterior to the ural is autogenous (a condition frequently noted on *Icichthys* larvae and juveniles). The nomeid caudal skeleton is illustrated by Haedrich (1967).

Branchiostegal rays form quite early; all six elements (2 + 4) are present on a 4.3-mm specimen. Gill rakers are beginning to form on the first arch on a 4.7-mm specimen, but the full complement is not yet developed on a 14.4-mm specimen.

Small, weakly developed preopercular spines are formed on early flexion larvae from ca. 4.5 mm and become embedded in a fringe of tissue at about 9.0 mm. These preopercular spines are difficult to see on material that is not cleared and stained.

A discussion of the development of teeth in *P. sio* in the late larval and early juvenile period is presented in an earlier section comparing dentition of pelagic stromateoid fishes.

Scales are first evident on the body of a 14.4-mm specimen. At this size, a full complement of 9 + 9 procurrent caudal rays is

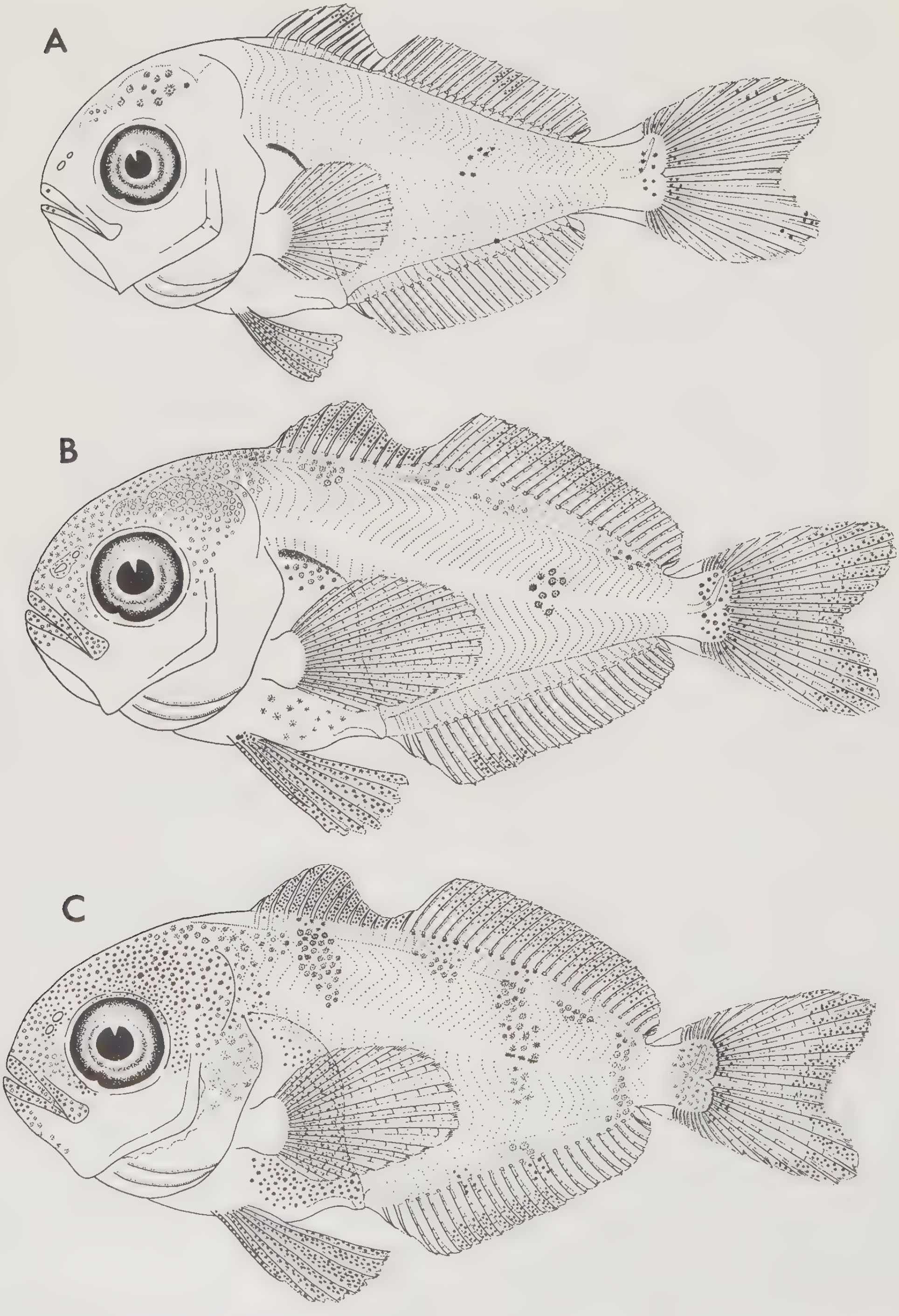

Figure 46. Developmental stages of *Psenes sio* (Nomeidae). A—7.6-mm postflexion larva; B—14.8-mm early juvenile; C—17.4-mm early juvenile.

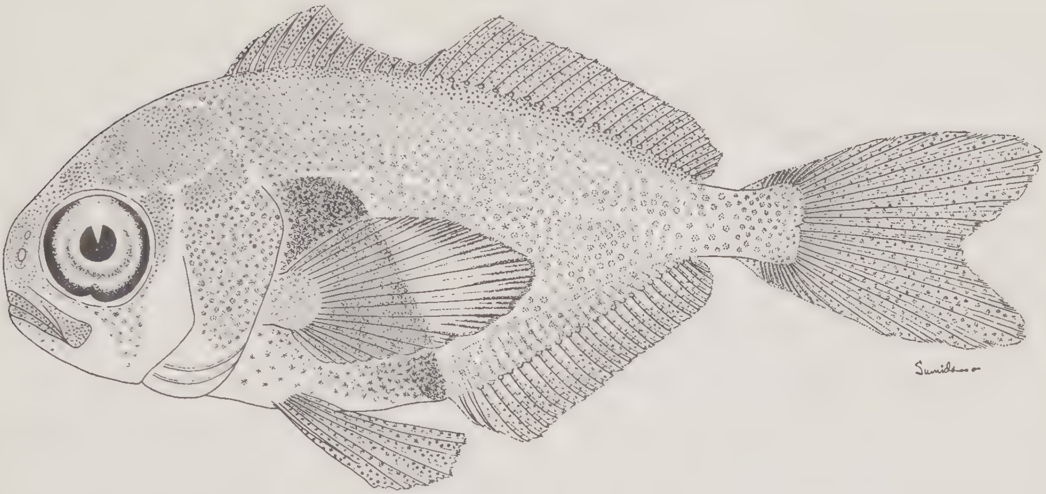

Figure 47. Juvenile of *Psenes sio* (Nomeidae), 26.9 mm.

completed along with the other fins, characters which make specimens at this size juveniles.

Pigmentation.—Larvae of *P. sio* are pigmented similarly to other *Psenes* at small sizes but with several diagnostic differences. The banding pattern developed on early juveniles of *Psenes sio* is transitory and is soon succeeded by uniform pigmentation on juveniles as small as 27 mm.

A 2.4-mm yolk-sac larva (Fig. 45A) has pigment similar to the late embryo (Fig. 2G). Pigment is present on the head anterior and posterior to the eye, above the gut near the oil globule and anterior to the anus, and below the gut anterior to the oil globule. Pigment on the body consists of lateral pigment above the oil globule, dorsal pigment at myomeres 13 and 14 and dorsal, ventral, and lateral pigment at myomeres 22 to 24.

Preflexion larvae, 2.1 to 3.6 mm long (Figs. 45B and C), have heavy pigment under the lower jaw in the form of an inverted "Y" (Fig. 29E), pigment at the cleithral symphysis, and on the peritoneum above the gut. The tail has three dorsal pigment patches, one at myomeres 12 to 14, a second at myomeres 22 to 24, and a third patch near the tip of the notochord. Under the second patch are lateral and ventral pigment patches, and under the third is a ventral pigment patch. There is a line of melanophores along the ventral margin of the tail. The early forming pelvic fins are pigmented.

Flexion larvae, 4.3 to 5.6 mm long (Figs. 45D and E), add little pigment to the preexisting pattern. By late flexion some pigment develops on the upper jaw and on the head above the eyes. The dorsal, ventral, and lateral body pigment at myomeres 24 and 25 is less accentuated than on some preflexion larvae. The anterior dorsal pigment spot is lost during flexion. The 13 to 19 ventral melanophores are still conspicuous but are becoming embedded by late flexion. The dorsal and ventral pigment near the tip of the notochord spreads over the developing hypurals and bases of the caudal rays.

Postflexion larvae and early juveniles, 6.0 to 17.4 mm long, develop conspicuous pigment on the head and fins and the banded pattern of the body (Fig. 46). The ventral line of melanophores persists until 7.6 mm (Fig. 46A). Pigment begins to form on the dorsal and caudal fin membranes at this size.

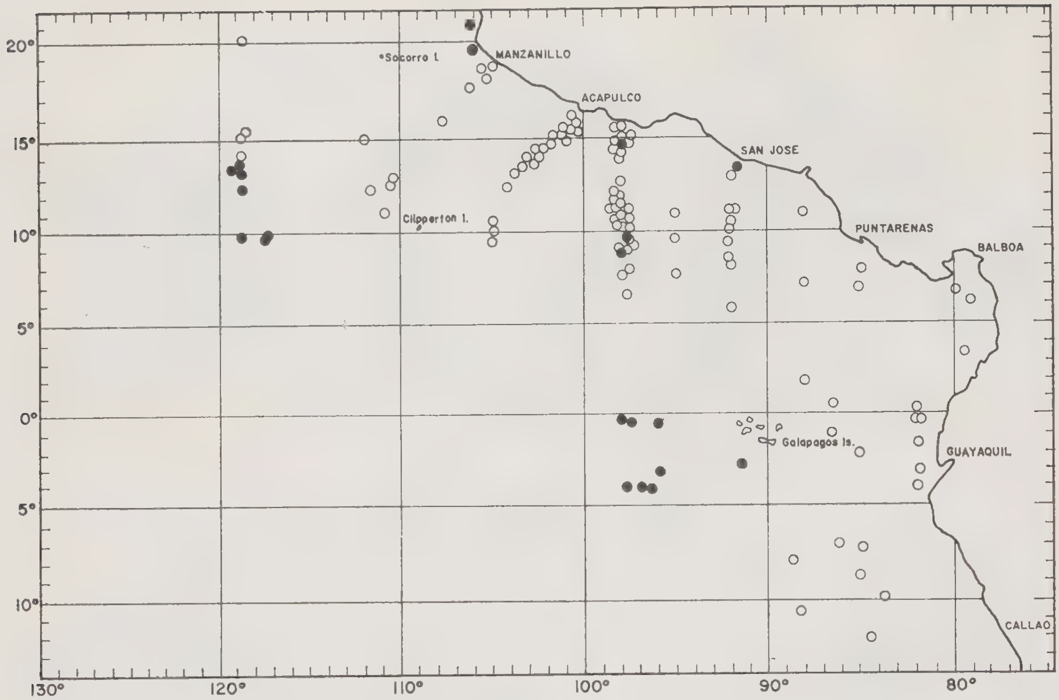

Figure 48. Occurrences of *Psenes sio* larvae (open circles) and juveniles (closed circles) in the eastern tropical Pacific.

The head becomes covered with pigment by 14.8 mm. A single pigment patch forms under the first dorsal fin. Three patches are formed under the second dorsal fin at 14.8 mm (Fig. 46B). By 17.4 mm (Fig. 46C), four patches are present under the second dorsal, about equally spaced between the origin and termination of this fin, with two of these patches spreading ventrally to form bands. In addition, the pigment over the hypural bones is heavy and spreads over to the adjacent caudal rays. On a 17.4-mm specimen, pigment is uniform on the pelvic and first dorsal fins, is present on the distal half of the second dorsal and caudal, and is patchy on the anal fin. Only the pectoral fins lack pigment.

Larger juveniles lose the banding pattern on the body formed earlier and become uniformly pigmented as illustrated for a 26.9-mm specimen (Fig. 47).

Distribution and Relative Abundance of Pelagic Stromateoid Fishes in the Eastern Pacific

Amarsipus carlsbergi is a tropical species. It occurred in the eastern tropical Pacific between 15°N to 3°S latitude, and 105° to 125°W longitude; it was also taken off Hawaii. In abundance it would be classed between rare and rather common.

The four centrolophids from the eastern Pacific are all temperate water forms. Larvae of *Icichthys lockingtoni* are commonly taken over much of the CalCOFI pattern; their primary distribution in the eastern Pacific is in the transition waters of the California Current. The three species of *Schedophilus* (*S. maculatus*, *S. huttoni*, and *S. labyrinthicus*) were all dipnetted under jellyfish from the eastern South Pacific; none of these was taken in more than two collections; hence each is quite rare.

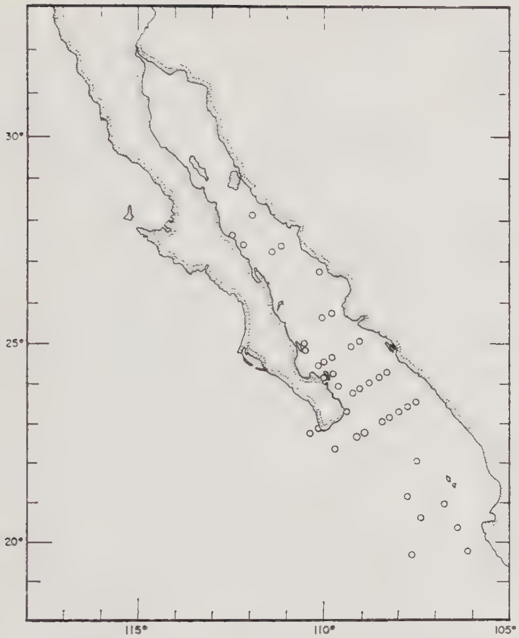

Figure 49. Occurrences of *Psenes sio* larvae in the Gulf of California and adjacent areas. Open circles indicate locality of collections.

The genus *Tetragonurus* has a wider latitudinal distribution than the other pelagic stromateoid genera. *T. cuvieri* is a temperate water form in the eastern Pacific occurring over an extensive area, including the offshore central water mass; it is moderately common. *T. atlanticus* is a tropical-subtropical species; most occurrences in the tropical eastern Pacific were in an oceanic band between 5°N and 5°S, although some specimens were obtained to 20°S. The other records for this species are from the central North Pacific, between Hawaii and the International Date Line to as far north as about 33°N. Such disjunct distributions undoubtedly result from sampling hiati rather than actual breaks in distribution. With regard to relative abundance, *T. atlanticus* would be classed between rare and rather common. We have only three specimens of *T. pacificus*, two from the tropical eastern Pacific and one from off Hawaii.

Nomeids are taken in tropical-subtropical waters, with the majority of occurrences within the tropics. Of the 11 kinds that have been collected from the eastern Pacific, four could be classed as quite rare (i.e., with one to three occurrences), one as rare (with five to 10 occurrences), three as rather comon, two as common, and only one as relatively abundant. Three of the species classed as quite rare are *Cubiceps* species: the southern occurring *C. capensis* (two occurrences), the tropical occurring *Cubiceps* sp. A (three occurrences), and the North Pacific central water mass form, *Cubiceps* sp. B (three occurrences). There is but a single occurrence of *Psenes maculatus* (20°N, 123°W). The rare form is *Nomeus gronovii* with seven occurrences. The forms classed as rather common are *Psenes pellucidus*, *P. arafurensis*, and *P. cyanophrys*; those classed as common are *Psenes sio*, which occurs in a broad coastal band in the eastern tropical Pacific extending into the Gulf of California, and the widely distributed *Cubiceps caeruleus*. The species most frequently taken was *Cubiceps pauciradiatus*, which perhaps also is the most common nomeid on a worldwide basis.

To give some quantitative assessment of the relative abundance of pelagic stromateoid larvae and juveniles, information is summarized for EASTROPAC cruises, particularly EASTROPAC I, and for collections taken off Hawaii. On EASTROPAC I, 961 specimens obtained at 178 of the 478 stations occupied were nomeid larvae, seven larvae from six stations were tetragonurids and five larvae from five stations were amarsipids. On EASTROPAC II, 1,460 specimens from 229 of 355 stations occupied were of nomeid larvae, 12 specimens from 11 stations were tetragonurid larvae and two specimens from two stations were amarsipid larvae. On both surveys, nomeid larvae contributed slightly over 1% of the total number of larvae of all kinds.

Of the nomeids taken on EASTROPAC I, 829 specimens were available for study. As mentioned in Ahlstrom (1971), eight kinds of nomeid larvae were taken on

EASTROPAC I. Of these, *Cubiceps pauciradiatus* was by far the most common with 706 specimens taken at 135 stations. *Psenes sio* was the next most common form with 69 specimens from 32 stations, followed by *C. caeruleus* with 25 specimens from 17 stations, *P. arafurensis* with 13 specimens from nine stations, *P. cyanophrys* with nine specimens from eight stations, *P. pellucidus* with five specimens from four stations, *Cubiceps* sp. A, one specimen and *Nomeus gronovii*, one specimen. A re-examination of *Tetragonurus* material of EASTROPAC I shows that only one species was represented, *T. atlanticus*, with seven specimens from six hauls. Single specimens of the monotypic *Amarsipus carlsbergi* were taken at five stations. Collections of juveniles and adults obtained in midwater trawl hauls made on NMFS cruises in the eastern tropical Pacific (TOWNSEND CROMWELL cruise 51 and DAVID STARR JORDAN cruises 57, 60, 65, and 77) contained the above 10 kinds of pelagic stromateoid fishes in roughly the same order of relative abundance as for larvae.

Juveniles of four species of nomeids were taken in midwater trawl hauls made off Hawaii on TOMNSEND CROMWELL cruise 32. The relative abundance of the four species was as follows: *Cubiceps pauciradiatus*—798 specimens taken in 45 hauls, largest collection with 119 specimens; *Psenes cyanophrys*—139 specimens taken in 31 hauls, largest collection with 19 specimens; *P. arafurensis*—39 specimens taken in 19 hauls, largest collection with five specimens; and *C. caeruleus*—six specimens taken in five hauls.

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ADDENDUM

A paper by T. A. Pertseva-Ostroumova and T. S. Rass, 1973, Ichthyoplankton of the South-eastern Pacific Ocean, Tr. Inst. Okeanol. Akad. Nauk. SSSR 94: 7-70, has been brought to our attention. They record and illustrate three kinds of stromateoid larvae. The series referred by them to *Cubiceps caeruleus* is shown by their illustrations to be *Cubiceps pauciradiatus*. The series referred to *Nomeus albula* (Meuschen)? appears to be a mixture. The largest specimen in the series, 10.0 mm, is that of *Nomeus gronovii*, the other five illustrations, including a late-stage egg and larvae 3.2, 3.4, 4.5 and 7.5 mm, are almost certainly *Psenes sio*. A 6.5-mm specimen of *Amarsipus carlsbergi* is illustrated.

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APPENDIX 1

Station Positions of Collections of Larvae and Early Juveniles Included in Morphometric and Meristic Tables

This appendix is included to provide information on the localities of capture (station position) and date of capture of the larvae and early juveniles included in morphometric and meristic tables. In these tables, specimens were utilized from 72 EASTROPAC stations, 54 CalCOFI stations, 36 stations from 11 expeditions or special cruises as follows: JORDAN cruises 57, 60, and 77 (all in the eastern tropical Pacific); TOWNSEND CROMWELL cruise 32 (off Hawaii) and cruise 51 (eastern tropical Pacific); and Scripps Institution of Oceanography expeditions designated NORPAC, SHELLBACK (S.B.), STEP I, CLIMAX II, CATO II, ARIES 9, and SOUTH TOW. Where no Scripps expedition or cruise name was given, the Scripps collection number is listed, e.g., SIO 64-641. (This is also done in the tables of juvenile and adult meristics.) Collections listed as "Hunter and Mitchell" were made off Costa Rica (Hunter and Mitchell, 1967, 1968). In addition, the samples designated "Hawaii" followed by a series of numbers were from a station off the Hawaiian Island of Oahu which was sampled repeatedly by Thomas Clarke (Clarke, 1973).

EASTROPAC (ETP) cruises: stations numbered 11.000 to 14.000 were taken on the first multivessel EASTROPAC cruise; 11.000 series by R/V ARGO (SIO), 12.000 series by R/V DAVID STARR JORDAN (BCF); 13.000 series by R/V ROCKAWAY (U.S. Coast Guard), and 14.000 series by R/V ALAMINOS (Texas A & M). Stations numbered 20.000, 30.000, 50.000, and 60.000 were all occupied on single vessel cruises made by R/V DAVID STARR JORDAN. Stations numbered 45.000 to 47.000 were taken on the second multivessel EASTROPAC cruise; 45.000 series by R/V THOMAS WASHINGTON (SIO), 46.000 series by R/V UNDAUNTED (BCF), and 47.000 series by R/V ROCKAWAY. From the third multivessel EASTROPAC cruises, collections are included from 75.000 series, taken by R/V Thomas Washington. The OP series was made on a transect through the EASTROPAC area by R/V Oceanographer (Environmental Science Service). Observations were numbered sequentially for each series.

The CalCOFI series were taken by no fewer than 10 research vessels. In designating CalCOFI samples the vessel is identified by a single letter that precedes the cruise and station designation. For example, station B5607-120.50 was taken from the R/V Black Douglas (B) on cruise 5607, i.e., 56 (year) and 07 (month) for July 1956, on station 120.50, one of the permanent CalCOFI grid stations—this one located about 40 miles offshore from Cedros Island, Baja California. The designation of CalCOFI research vessels by letters in the tables are as follows: B, Black Douglas (BCF); C, Crest (SIO); G, Alexander Agassiz (SIO); H, Horizon (SIO); J, David Starr Jordan (NOAA); L, Alaska (CF&G); O, Orca (SIO); P, Paolina T. (SIO); S, Stranger (SIO); and Y, Yellowfin (CF&G). The vessel is indicated before each station in the text tables, but not in the following appendix tables.

The collections from off Hawaii were obtained on Townsend Cromwell (T.C.) cruise 32 or from a series of hauls made at a station off Hawaii by Thomas Clarke. The latter are designated as Hawaii—followed by station data, as for example: Hawaii 71-9-3 identifies a haul made in 1971 (71), during September (9) which was the third of a series of hauls taken during this cruise. The Clarke series were made from R/V Teritu (University of Hawaii) in an area bounded by 21°20′ to 21°35′N latitude and 158°20′ to 158°35′W longitude. Cruise designated 70-9 was made on September 14-17 and 20-24, 1970; 71-6 on June 8-11 and 15-19, 1971; 71-9 on September 17-19, 1971; and 71-10 on October 4-6, 1971.

The collections taken on expeditions need no amplification.

Appendix Table 1A. Station positions of EASTROPAC (ETP) collections included in morphometric and meristic tables for larvae

	Station position		
Station	Latitude	Longitude	Date
11.066	06°49.8′N	118°55.5′W	II. 3.67
068	06°05.0′N	118°51.0′W	II. 3.67
098	00°05.8′N	119°00.0′W	II. 6.67
114	02°37.8′S	119°02.3′W	II. 7.67
213	11°13.7′S	126°01.0′W	II.19.67
306	12°03.5′N	126°00.0′W	II.27.67
12.026	17°24.5′N	106°17.0′W	II.15.67
094	00°10.0′S	105°00.0′W	II.26.67
221	00°44.0′S	112°01.5′W	III.13.67
224	00°20.0′S	112°00.0′W	III.13.67
246	06°12.0′N	112°00.5′W	III.16.67
13.019	11°22.5′N	88°05.0′W	II. 4.67
048	04°41.0′N	91°58.0′W	II.11.67
052	03°25.0′N	91°58.0′W	II.11.67
056	01°58.0′N	92°08.5′W	II.12.67
079	06°59.0′S	92°05.0′W	II.17.67
105	15°45.0′S	92°07.0′W	II.20.67
117	19°52.0′S	92°05.0′W	II.21.67
191	02°26.0′S	97°57.0′W	III. 2.67
241	07°19.0′N	98°03.0′W	III. 5.67
243	08°05.0′N	97°59.0′W	III. 5.67
14.001	06°52.0′N	79°44.0′W	I.31.67
209	07°50.0′N	85°59.3′W	III.14.67
20.064	00°02.0′S	119°17.0′W	IV.20.67
100	05°19.0′N	112°28.0′W	IV.26.67
191	03°27.0′N	105°22.0′W	V.13.67
193	02°46.0′N	105°29.0′W	V.13.67
195	02°13.0′N	105°23.0′W	V.13.67
222	01°11.0′N	98°05.0′W	V.18.67
224	02°04.0′N	98°10.0′W	V.19.67
30.043	07°51.0′N	118°24.0′W	VI.22.67
055	03°47.0′N	118°30.0′W	VI.23.67
083	01°22.0′S	111°32.0′W	VI.29.67
248	09°22.0′N	97°31.0′W	VII.25.67
45.028	16°11.3′N	119°03.3′W	VIII. 9.67
090	00°57.2′N	119°04.5′W	VIII.16.67
125	04°45.8′S	118°53.0′W	VIII.19.67
45.131	06°19.5′S	118°58.0′W	VIII.19.67
177	05°21.1′S	111°59.5′W	VIII.25.67
325	09°01.8′N	111°54.8′W	IX. 6.67
358	17°20.5′N	106°29.8′W	IX.10.67
46.059	00°24.0′N	105°25.0′W	VIII.24.67
071	03°17.0′S	104°55.0′W	VIII.25.67
124	12°53.0′N	98°03.0′W	IX. 5.67
47.244	06°59.0′N	84°54.0′W	VIII.27.67
246	07°42.5′N	85°04.0′W	VIII.27.67
297	04°38.0′N	87°57.5′W	IX. 4.67
50.055	03°39.0′N	119°15.5′W	X.26.67
061	02°08.5′N	119°28.0′W	X.27.67
071	01°04.4′S	119°13.0′W	X.28.67
077	02°59.0′S	112°10.0′W	X.30.67
082	01°02.5′S	112°13.2′W	X.31.67
090	02°02.4′N	112°15.0′W	XI. 1.67
170	07°29.5′N	105°10.5′W	XI.14.67
234	08°47.0′N	98°05.0′W	XI.24.67
238	10°17.0′N	98°06.0′W	XI.25.67
60.060	03°01.0′N	118°43.0′W	XII.28.67
062	02°33.0′N	118°44.0′W	XII.28.67
072	00°51.0′N	118°39.0′W	XII.29.67
078	00°15.0′S	118°38.0′W	XII.30.67
093	02°58.0′S	111°46.0′W	I. 2.68
150	14°51.0′N	108°55.0′W	I. 7.68
189	09°13.0′N	104°46.5′W	I.16.68
195	06°58.0′N	104°46.5′W	I.17.68
276	06°54.0′N	97°44.5′W	I.26.68
75.048	03°33.0′N	118°52.0′W	II.25.68
064	00°44.0′N	118°58.0′W	II.26.68
068	00°00.0′N	118°54.0′W	II.26.68
198	03°19.0′N	98°05.0′W	III.23.68
239	05°00.0′N	98°02.0′W	IV. 4.68
241	06°22.0′N	98°01.0′W	IV. 5.68
OP 044	01°57.0′S	84°58.0′W	XI.18.67

Appendix Table 1B. Station positions of CalCOFI collections included in morphometric and meristic tables for larvae

	Station position		
Station	Lat. N	Long. W	Date
4903-81.127	31°47.0′	125°38.0′	III.14.49
5202-80.90	33°09.0′	123°13.0′	II.21.52
5203-90.53	32°37.5′	119°31.0′	III. 9.52
5412-107.40	30°10.0′	116°43.0′	XII.13.54
5603-110.80	28°16.5′	118°59.0′	III.16.56
5604-83.60	33°33.5′	120°45.0′	IV.16.56
5604-107.50	29°53.5′	117°23.0′	IV.26.56
5607-120.50	27°33.0′	115°52.5′	VII.13.56
5611-93.55	32°01.5′	119°16.0′	X.31.56
5612-170.20	20°32.0′	107°28.5′	XII. 2.56
5612-173.30	20°20.5′	106°31.0′	XII. 5.56
5701-100.60	30°39.5′	118°50.0′	I.19.57
5702-107.60	29°31.0′	118°03.0′	II.19.57
5706-153.20	22°48.0′	110°22.0′	VI. 7.57
5706-153.25	22°37.0′	110°40.0′	VI. 7.57
5706-157.25	21°55.0′	110°16.0′	VI. 8.57
5805-77.50	34°05.0′	120°52.0′	V.11.58
5905-70.75	35°24.0′	123°27.5′	V.19.59
5905-73.80	34°33.5′	123°27.5′	V.18.59
5908-110.55	29°07.0′	117°18.0′	VIII.22.59
5908-113.45	28°52.0′	116°18.0′	VIII.20.59
6001-157.25	22°02.5′	110°19.0′	I.27.60
6101-77.55	34°56.0′	121°17.5′	I. 6.61
6107-80.60	34°09.0′	121°09.0′	VI.30.61
6107-83.80	32°55.5′	122°05.0′	VII.13.61
6204-60.80	36°54.0′	125°05.0′	III.27.62
6204-70.80	35°15.0′	123°49.0′	III.21.62
6204-80.100	32°57.0′	123°56.0′	III.18.62
6204-113.50	28°41.0′	116°35.0′	IV.22.62
6207-87.65	32°50.0′	120°41.5′	VII.12.62
6207-87.90	32°02.0′	122°23.0′	VII.11.62
6207-90.80	31°45.0′	121°19.5′	VIII.28.62
6207-90.120	30°24.5′	123°59.5′	VIII.27.62
6207-93.90	30°50.0′	121°34.5′	VII.16.62
6210-80.100	32°54.5′	123°56.0′	X.12.62
6301-80.80	33°27.5′	122°32.5′	I.14.63
6310-80.80	33°28.5′	122°32.5′	X. 3.63
6310-83.60	33°34.0′	120°45.0′	X. 4.63
6410-93.90	30°51.0′	121°35.0′	X.11.64
6509-113.40	29°02.0′	115°57.0′	IX.16.65
6604-73.53	35°31.0′	121°28.5′	IV. 7.66
6607-93.80	31°10.0′	120°54.5′	VII.27.66
6707-90.120	30°23.0′	124°00.0′	VI.29.67
6707-93.140	29°09.0′	124°52.5′	VI.30.67
6707-107.65	29°18.5′	118°21.0′	VII. 9.67
6907-73.65	35°08.0′	122°19.0′	VII.23.69
7205-20.129	20°00.0′	129°00.0′	V.27.72
7205-157G130	23°33.5′	107°31.1′	VI. 7.72
7210-31.135	31°00.0′	135°00.0′	IX.30.72
7210-31.139	31°00.0′	139°00.0′	X. 2.72
7210-31.145	31°00.0′	145°00.0′	X. 3.72
7210-24.143	24°00.0′	142°50.0′	X.30.72
7210-20.123	20°00.0′	123°06.0′	XI. 6.72

Appendix Table 1C. Station positions of collections obtained on special cruises or expeditions

Expedition and station	Station position		Date
	Latitude	Longitude	
Shellback 115	08°16.0′S	83°42.0′W	VII. 2.52
Shellback 150	07°10.5′S	84°58.0′W	VII.26.52
Shellback 154	02°59.0′S	85°00.5′W	VII.27.52
Shellback 155	01°56.0′S	84°59.5′W	VII.28.52
Shellback 162	04°55.0′N	85°01.0′W	VII.30.52
Shellback 178	01°10.0′N	89°28.0′W	VIII. 8.52
NORPAC 95	30°20.5′N	119°27.0′W	IX.16.55
NORPAC 107	29°50.0′N	115°51.0′W	IX.21.55
Step 1 32	18°06.0′S	80°56.0′W	X.31.60
Step 1 40	20°37.0′S	76°51.0′W	XI. 5.60
Jordan 57.030	09°43.5′N	119°30.0′W	XI.12.70
Jordan 57.035	10°00.0′N	119°00.0′W	XI.12.70
Jordan 57.047	10°46.0′N	117°28.0′W	XI.15.70
Jordan 57.113	07°14.6′N	119°24.0′W	XII. 7.70
Jordan 60.150	09°27.7′N	117°49.0′W	IV. 7.71
Jordan 77.101	04°21.5′N	118°14.8′W	I.28.73
Jordan 77.119	07°30.0′N	117°20.4′W	I.31.73
Jordan 77.144	10°00.0′N	122°19.0′W	II. 4.73
Jordan 77.155	09°31.2′N	123°18.0′W	II. 6.73
Cromwell 51.048	04°02.0′S	118°48.0′W	XI. 8.70
Cromwell 51.056	03°12.0′S	119°26.0′W	XI.10.70
Cromwell 51.063	03°44.0′S	119°30.0′W	XI.12.70
Cromwell 51.066	03°10.0′S	120°19.5′W	XI.12.70
Cromwell 51.071	03°12.0′S	121°27.0′W	XI.14.70
Cromwell 51.081	02°10.0′N	121°37.0′W	XI.17.70
Cromwell 51.082	01°56.0′N	121°41.0′W	XI.18.70
Cromwell 32.010	21°22.0′N	158°15.0′W	VII.15.67
Cromwell 32.012	21°23.0′N	158°15.0′W	VII.16.67
Cromwell 32.023	21°00.0′N	158°30.0′W	VII.22.67
Cromwell 32.034	21°01.0′N	158°32.0′W	VII.14.67
Climax II (dipnet)	24°42.0′S	155°03.5′W	X. 3.69
Climax II (dipnet)	24°34.0′S	154°50.0′W	X. 9.69
Cato II B3.119	25°14.8′S	155°07.7′W	VIII. 1.72
Aries 9 H-17	27°28.2-27.0′N	155°28.6-47.0′W	X. 2.71
Aries 9 A-2	27°22.4-11.8′N	155°01.2-02.9′W	IX.24.71
South Tow Sta. 13	28°07.0-18.3′N	155°07.8-14.9′W	II.6-7.73
Hunter & Mitchell	09°45.0′N	85°39.0′W	V.14.66

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DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES OF THE COMMERCIAL LANTERNFISH, *LAMPANYCTODES HECTORIS* (GÜNTHER), OFF THE WEST COAST OF SOUTHERN AFRICA WITH A DISCUSSION OF PHYLOGENETIC RELATIONSHIPS OF THE GENUS

Elbert H. Ahlstrom[1], H. Geoffrey Moser[1], and Michael J. O'Toole[2]

Abstract: *Lampanyctodes hectoris* is a species of lanternfish which is becoming an important part of the pelagic fishery off South Africa. The Southwest Africa Pelagic Egg and Larval Survey has provided an abundance of larval specimens of this species. The larvae, transitional and early juvenile stages are described and illustrated for the first time and information on their distribution and relative abundance is provided. Larval characters are used in combination with selected adult characters to elucidate the phylogenetic affinities of this genus.

Lanternfishes of the family Myctophidae are the most ubiquitous and speciose (approximately 250 species in 30 genera) of all fishes in the oceanic mid-waters. Although their total biomass is unknown, the fact that lanternfishes, on the average, make up approximately one-half of all fish larvae taken in any oceanic plankton tow gives some impression of its immensity. Although they are small fishes, usually less than 100 mm in length, they may have the greatest biomass of any vertebrate family. Knowledge of their ecological role in the world ocean is poor, but initial studies suggest that these fishes are a major element in the oceanic food web. Among the commercially important organisms known to prey on lanternfishes are salmon (Shimada, 1948; Manzer, 1968), tunas (Alverson, 1963; Pinkas et al., 1971), rockfish (Pereyra et al., 1969), fur seals (Mead and Taylor, 1953) and cetaceans (Fitch and Brownell, 1968). Recent studies (Paxton, 1967; Holton, 1969; Legand and Rivaton, 1969; Collard, 1970; Baird et al., 1975) indicate that lanternfishes are important grazers on herbivorous zooplankton.

Historically, lanternfishes have not been commercially exploited because of their small size and relatively diffuse distribution in the water column. A growing body of observations indicates that some species of lanternfishes aggregate in large numbers at certain times during their life cycles and, at such times, may be available to a fishery. There have been several well-documented observations of lanternfish swarming at the surface in dense "balls." *Benthosema panamense* exhibits this behavior during daylight in the eastern Pacific and tuna boat skippers report that yellowfin and skipjack tuna feed exclusively on these swarms when they are observed (Alverson, 1961). Similar swarms of *Diaphus garmani* were reported at night in the central Pacific (Nakamura, 1970). Lanternfishes also aggregate in extensive shoals. Observations from submarines indicate that some species of lanternfishes, such as *Ceratoscopelus maderensis* (Backus et al., 1968) and *Benthosema panamense* (Barham, 1971), form extensive aggregations in slope waters. G. Krefft (Institut für Seefischerei, Hamburg, pers. comm.) has achieved catch rates of 1¼ metric tons/hour of *Diaphus dumerili* with a commercial herring trawl off Buenos Aires. It is well known that myctophids are often a major element in deep scattering layers of the ocean (Barham, 1966; Pearcy and Mesecar, 1971). Additional knowledge of these phenomena may lead to the commercial harvesting of lanternfishes.

Recently a fortuitous fishery for the lanternfish *Lampanyctodes hectoris* has developed incidental to the anchovy/pilchard fishery off the western coast of South Africa (Centurier-Harris, 1974). Annual landings of lanternfishes (mostly *L. hectoris*) were 1,134 metric tons or 0.3 percent of the pelagic fishery catch in this region in 1969 and increased to 42,560 metric tons or 10.45 percent of the catch in 1973. The location of the fishery is shown in figure 1. This species is particularly desirable because of its high content (20 percent by weight) of fine quality oil.

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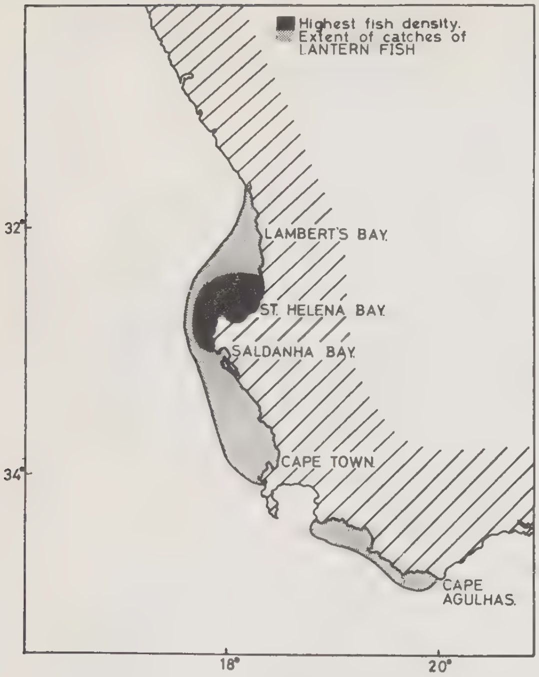
Highest fish density.
Extent of catches of LANTERN FISH
LAMBERT'S BAY
ST. HELENA BAY
SALDANHA BAY
CAPE TOWN
CAPE AGULHAS
32°
34°
18°
20°

Figure 1. Region of the fishery for *Lampanyctodes hectoris* off South Africa (from Centurier-Harris, 1974).

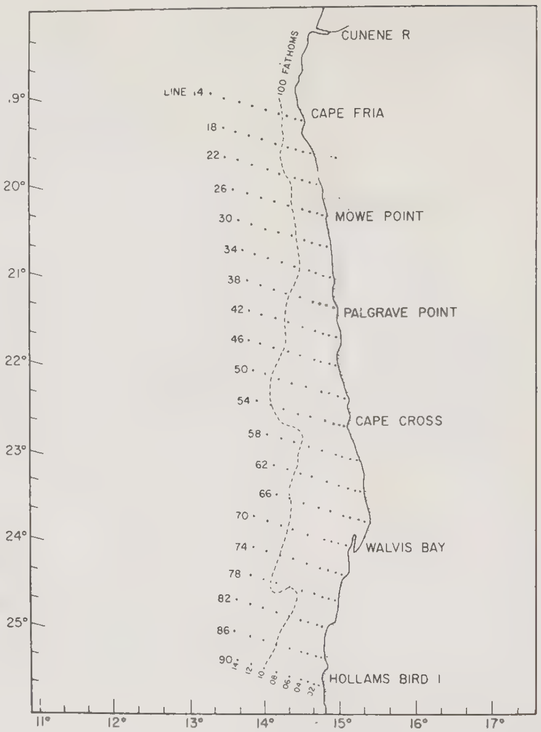
CUNENE R
100 FATHOMS
LINE 14
CAPE FRIA
MOWE POINT
PALGRAVE POINT
CAPE CROSS
WALVIS BAY
HOLLAMS BIRD I
18
22
26
30
34
38
42
46
50
54
58
62
66
70
74
78
82
86
90
19°
20°
21°
22°
23°
24°
25°
11°
12°
13°
14°
15°
16°
17°

Figure 2. Station plan for Southwest African Pelagic Egg and Larval Survey (SWAPELS).

Little is known about the life history of this important species of lanternfish. However, an extensive plankton survey, the Southwest African Pelagic Egg and Larval Survey (SWAPELS), was initiated by the Sea Fisheries Branch in 1972 (O'Toole, 1974). Although the data from this survey are not completely analyzed, some information on the distribution and relative abundance of *L. hectoris* larvae will be presented in this paper, the principal purpose of which is to describe the larval, transitional, and early juvenile stages of *L. hectoris*. Previously, Moser and Ahlstrom (1972) illustrated a 9.2 mm larva of *L. hectoris* and gave a partial description of the sequence of photophore formation based on the few specimens available. Examination of the abundant larval specimens from SWAPELS has shown that Moser and Ahlstrom (1972) were in error and that their 9.2 mm larva was *Lampadena* sp. The larvae of *Lampanyctodes hectoris* have a unique generic morph, a concept discussed extensively by Moser and Ahlstrom (1970, 1972, 1974). A number of larval characters give insight into the relationships of this genus with other myctophid genera and these will be treated in the discussion section of this paper.

METHODS

Specimens for the developmental part of this study were obtained from two plankton surveys of SWAPELS (Fig. 2). Survey 1 was carried out from August 1972 to March 1973 and Survey 2 from August 1973 to April 1974. The net used on both surveys was a 57 cm bongo net; 0.940 mm and 0.940 mm mesh were paired on Survey 1 and 0.940 mm was used on the left unit and 0.500 mm on the right on Survey 2. Oblique tows were made to a depth of 50 m at all stations except where the bottom was shallower than 50 m.

Techniques used for describing the development of *L. hectoris* are outlined in Moser and Ahlstrom (1970).

Lampanyctodes hectoris (Günther)
Figures 3 and 4

Literature.—The illustration of the 9.2 mm larva of *Lampanyctodes hectoris* and the remarks on photophore formation in that species in Moser and Ahlstrom (1972) are in error and refer to a larva of *Lampadena* sp. There are no illustrations or descriptions of *L. hectoris* larvae in the literature.

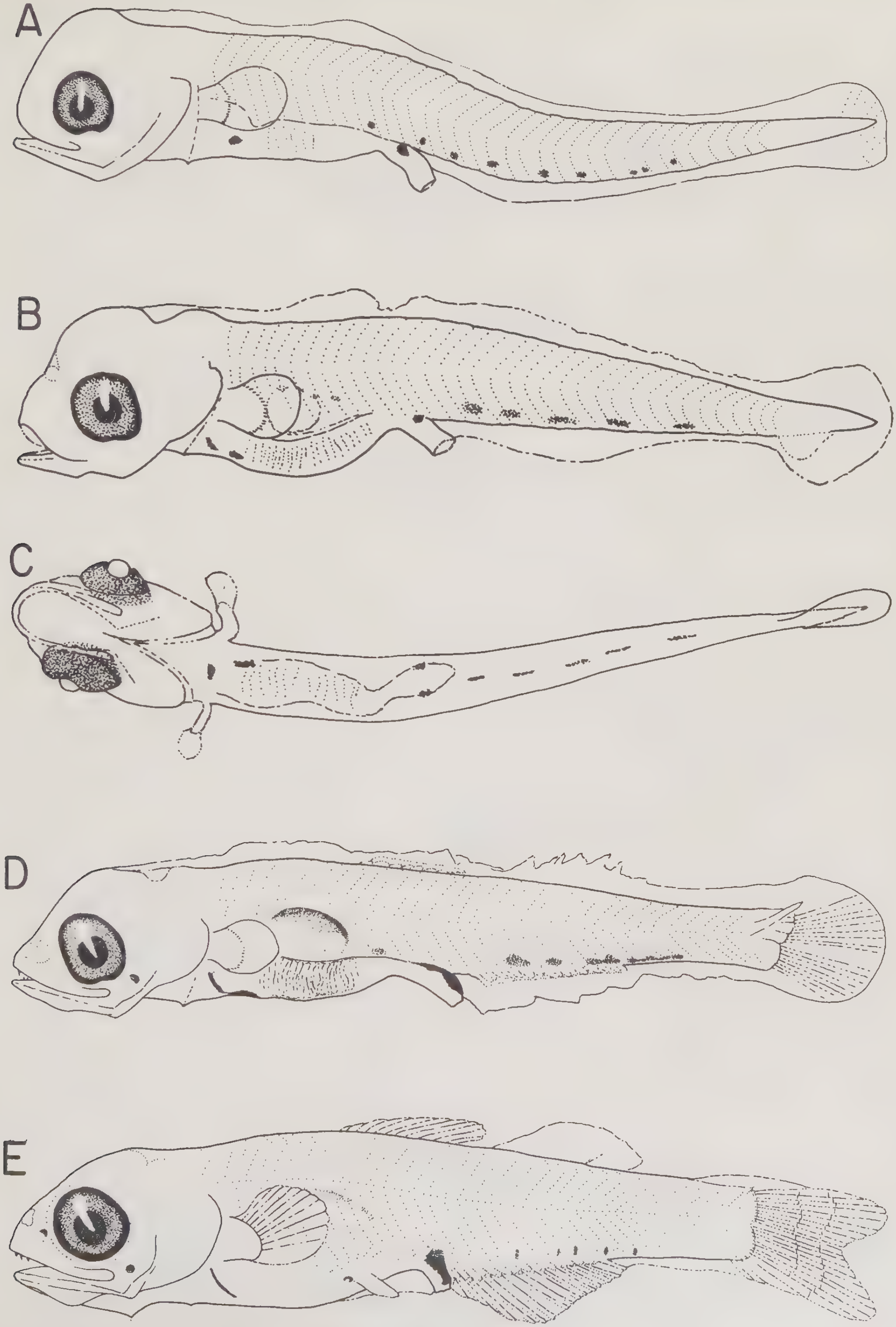

Figure 3. Larvae of *Lampanyctodes hectoris*. A. 3.8 mm; B. 5.0 mm; C. 5.0 mm, ventral view; D. 6.8 mm; E. 8.7 mm.

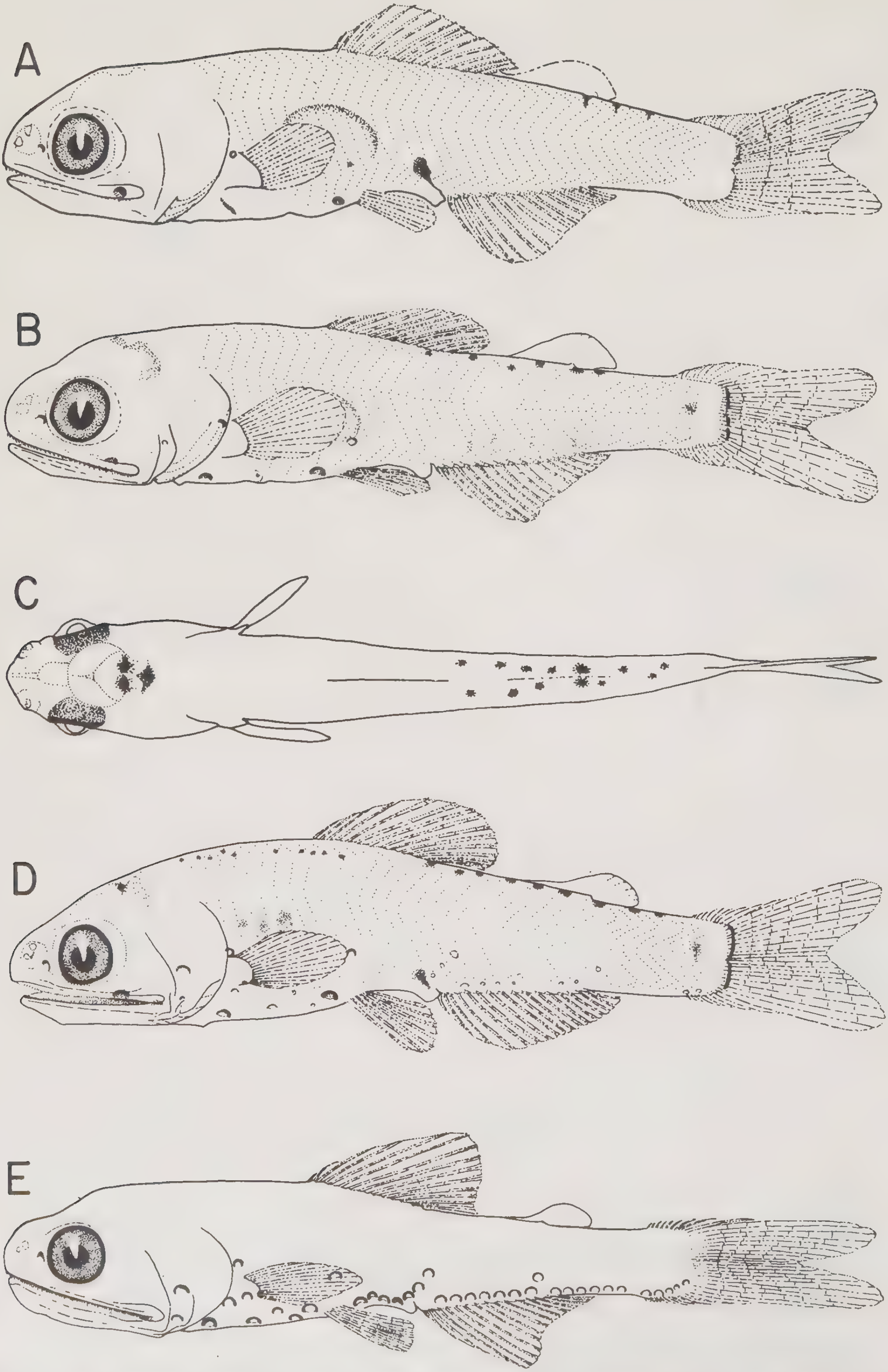

Figure 4. Developmental stages of *Lampanyctodes hectoris.* A. 11.7 mm larva; B. 13.0 mm larva; C. 13.0 mm larva, dorsal view; D. 14.9 mm transforming specimen; E. 14.2 mm juvenile.

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TABLE 1. Measurements (mm) of larvae of *Lampanyctodes hectoris.* (Specimens between dashed lines are undergoing notochord flexion).

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
3.8	1.8	0.75	0.50	0.15	0.23	0.29	–	0.49	0.20	–	–	–
4.0	1.8	0.72	0.43	0.12	0.20	0.27	–	0.43	0.19	–	–	–
4.3	2.0	0.85	0.52	0.16	0.24	0.30	–	0.45	0.25	–	–	–
4.5	2.3	0.96	0.53	0.20	0.27	0.31	–	0.63	–	–	–	–
4.8	2.5	1.0	0.70	0.26	0.29	0.37	–	0.68	0.29	–	–	–
5.0	2.6	1.2	0.75	0.25	0.38	0.43	0.02	0.85	0.20	–	–	–
5.2	2.7	1.1	0.70	0.27	0.31	0.39	–	0.73	0.35	–	–	–
5.6	2.8	1.2	0.77	0.35	0.34	0.42	0.01	0.82	0.25	–	–	–
5.8	3.1	1.4	0.78	0.32	0.38	0.46	0.01	0.86	0.36	–	–	–
6.0	3.1	1.2	0.80	0.32	0.41	0.48	0.02	0.88	0.26	–	–	–
6.2	3.2	1.4	0.83	0.33	0.43	0.48	0.04	1.0	0.33	2.4	–	–
6.4	3.7	1.4	0.90	0.34	0.49	0.55	0.03	1.1	0.27	2.8	–	–
6.6	3.8	1.7	1.0	0.45	0.53	0.62	0.04	1.2	0.32	2.8	3.9	3.0
6.8	4.0	1.7	1.0	0.36	0.57	0.55	0.01	1.2	0.28	3.0	4.2	2.8
7.0	4.0	1.7	1.1	0.40	0.52	0.63	0.02	1.2	0.56	3.1	4.2	3.2
7.2	4.2	1.9	1.0	0.40	0.57	0.68	–	1.4	0.46	3.1	4.3	3.2
7.5	4.2	1.8	1.0	0.43	0.52	0.62	0.03	1.3	0.57	3.2	4.3	3.3
7.7	4.6	1.9	1.0	0.40	0.64	0.71	0.04	1.3	0.52	3.3	4.6	3.2
8.0	4.6	2.0	1.2	0.45	0.61	0.71	–	1.5	0.60	3.3	4.7	3.3
8.2	4.9	2.2	1.2	0.49	0.68	0.75	0.02	1.6	0.65	3.8	4.9	3.6
8.7	5.0	2.3	1.3	0.50	0.77	0.87	0.02	1.8	0.87	3.8	5.0	3.8
9.2	5.2	2.2	1.2	0.60	0.73	0.84	–	1.8	1.0	4.2	5.3	4.1
9.7	5.7	2.5	1.3	0.68	0.73	0.86	–	2.0	1.0	4.2	5.7	4.2
10.1	6.2	2.9	1.4	0.71	0.87	0.91	–	2.2	1.2	4.6	6.2	4.5
10.5	6.5	2.9	1.6	0.73	0.88	1.0	–	2.3	1.2	4.8	6.5	4.8
10.8	6.7	3.0	1.7	0.78	0.83	0.95	–	2.4	1.4	5.1	6.7	4.8
11.0	6.8	3.0	1.6	0.74	0.79	0.95	–	2.3	1.3	5.0	6.9	4.8
11.7	7.1	3.3	1.7	0.93	0.87	1.0	–	2.6	1.5	5.4	7.1	5.2
12.0	7.5	3.3	1.8	0.83	1.0	1.1	–	2.8	1.5	5.7	7.5	5.3

TABLE 1. (*Continued*)

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
12.3	7.4	3.4	1.8	0.80	1.0	1.0	–	2.9	1.4	5.5	7.4	5.4
13.0	7.8	3.6	2.2	0.90	1.0	1.2	–	2.9	1.7	5.8	7.8	5.8
13.8	8.3	3.7	2.0	0.96	0.98	1.0	–	3.2	1.8	6.2	8.4	6.2
14.0	8.9	4.1	1.9	0.93	1.1	1.2	–	3.2	1.6	7.0	9.1	6.1
14.9*	8.8	4.0	2.2	0.95	1.1	1.2	–	3.7	2.1	6.6	8.8	6.4
14.2**	8.6	4.6	2.0	1.0	1.2	1.2	–	3.2	1.9	6.8	8.8	6.7
16.0**	9.8	5.0	2.8	0.94	1.3	1.3	–	3.5	2.5	7.2	9.9	7.1
21.2**	13.0	6.6	3.2	1.0	2.0	2.0	–	4.9	4.0	9.8	13.0	9.5

* Transforming specimen.
** Juvenile.

TABLE 2. Meristics from cleared and stained larvae of *Lampanyctodes hectoris*.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
7.5	7	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.7	10	9	0	1	3	3	5	5	–	–	–	–	5	–	–	–	–
8.3	10	9	–	–	3	3	4	5	–	–	–	–	7	–	–	–	–
8.7	10	9	2	3	4	4	7	7	1	3	–	–	11	7	–	–	–
9.2	10	9	3	4	5	5	9	9	2	3	–	–	13	9	4	4	–
9.6	10	9	4	5	6	6	10	9	4	3	–	–	14	12	5	5	–
10.1	10	9	5	6	7	7	12	12	4	3	–	–	15	12	7	7	–
10.5	10	9	6	7	7	7	11	11	4	3	–	–	16	13	7	7	–
11.1	10	9	7	8	8	8	11	12	4	3	–	–	16	13	7	7	26
11.8	10	9	7	8	8	8	13	13	4	3	0	12	16	14	8	8	37
12.3	10	9	–	9	7	8	–	12	4	3	5	14	15	14	8	8	37
12.7	10	9	9	11	9	9	13	13	4	3	8	17	16	14	8	8	37
13.2	10	9	9	10	9	9	12	12	4	3	4	13	16	14	8	8	37
14.4	10	9	8	9	10	10	13	12	4	3	10	17	16	14	8	8	37
15.9	10	9	10	10	9	9	13	13	4	3	10	20	16	14	8	8	37

Diagnostic features.—As for other species of lanternfishes, the pelagic eggs of *L. hectoris* are not known. The smallest larvae in our collection were 3.8 mm. Larvae obtain a moderate size in comparison with those of related genera. The largest larva in our collection is 14.4 mm and the smallest juvenile is 14.2 mm SL. A 14.9 mm specimen is undergoing transformation. Larvae of *L. hectoris* have a unique sequence of photophore development, beginning with the Br_2 in 6 mm larvae and followed by the Vn in 7 mm larvae, the PO_5 in 8 mm larvae, and the PLO and PO_1 in 11 mm larvae. Although several other genera develop this same complement of early-forming photophores, as explained in detail in a later section, none develops them in this sequence. Small larvae which have not developed photophores may be identified by their pattern of melanophores, the most characteristic of which are a persistent series of four to eight ventral tail melanophores, two melanophores in the foregut region, a bilateral pair at the divergence of the terminal region of the gut, a series of embedded spots above the mid-gut, and a melanistic shield above the developing gas bladder. In mid- and late-stage larvae, a bilateral series of melanophores develops on the posterior dorsum.

Morphology.—Larvae of *L. hectoris* have no striking morphological features. Body depth increases from a mean of 14 percent of the body length in preflexion larvae, to 18 percent in larvae undergoing flexion, to 22 percent in postflexion larvae and 23 percent in newly transformed juveniles (Table 1). Snout-anus length averages 50 percent of the body length in preflexion larvae, 58 percent during flexion and 60 percent in later developmental stages. Head size is moderate; relative head length increases gradually from a mean of 21 percent of body length in preflexion larvae to 25 percent during flexion, 27 percent in postflexion larvae and 31 percent in early juveniles. Relative head width decreases gradually during development; it averages 62, 58, and 54 percent of the head length for the three major larval stages and 49 percent in early juveniles. Snout length is moderate, averaging 24 percent of the head length over the entire larval period and shortens to 19 percent in early juveniles. The eye is moderately large; eye length averages 36 percent of the head length in larvae up to the completion of notochord flexion, is reduced to a mean of 33 percent in postflexion larvae and further to 27 percent in early juveniles. The eye is slightly elliptical in preflexion larvae; eye width averages 82 percent of eye length, but this increases to a mean of 89 percent in later larval stages and the eyes of early juveniles are round. There is a sliver of ventral choroid tissue that appears in larvae between 5.0 and 9.0 mm. It reaches a maximum relative depth of 8 percent of the eye length and is only slightly paler in color than the eye itself.

Ossification of some important larval features is as follows. Vertebrae begin to ossify at about 11.1 mm length and the full complement of 36 to 37 is ossifying in larvae 12.3 mm and larger. Branchiostegal rays begin to ossify in 7 mm larvae, but, the full complement of 11 as listed by Paxton (1972) is not achieved in larvae nor in the earliest juveniles.

The maxillary is ossifying in larvae as small as 3.9 mm but develops no teeth. The dentary is ossifying and bearing teeth by 5.9 mm, as is the premaxillary. Teeth are uniserial on the premaxillary with the anterior five or six teeth larger than the remainder; as many as 20 conical, usually straight teeth form on late-stage larvae. On the posterior two-thirds of each dentary bone a series of six to eight conspicuous hooked teeth form early in the larval period. The hooked part of each tooth projects anteriad at almost right angles to the base of the tooth. They persist to transformation. The dentary teeth anterior to these, and later between and posterior to the hooked teeth, are conical, straight and uniserial anteriorly. Late-stage larvae have more than 30 such dentary teeth. The hooked and uniserial teeth present on the jaws of larvae are shed or resorbed and replaced by the wide bands of numerous small teeth at transformation.

Fin formation.—A pectoral fin with differentiated base and blade is present in our smallest larvae (3.8 mm). The base remains small and inconspicuous throughout the larval period as does the blade, which has a rounded posterior margin. At transformation the pectorals extend posteriad to the origin of the pelvics. Rays begin to ossify in 7 mm larvae in a dorsal to ventral sequence and the full complement of 13 to 14 is present in larvae as small as 11.8 mm (Table 2).

The anlage of the caudal fin is present in larvae as small as 5.0 mm. The principal caudal rays begin to ossify in 7 mm larvae and the full complement of 10+9 rays is ossifying in a 7.7 mm specimen. Procurrent caudal rays also begin to ossify in 7 mm larvae and the full complement of 8 to 10 superior and 9 to 11 inferior rays is ossifying in 12 mm larvae. The hypural elements begin to ossify in 8 mm larvae and the full complement of four superior and three inferior elements is ossifying in 9 mm larvae. Flexion of the notochord begins when the larvae are about 6.5 mm long and is completed at about 8.0 mm length.

The anal and dorsal fin bases begin to form during notochord flexion. Anal fin rays are beginning to ossify in a 7.7 mm larva and dorsal rays are ossifying in an 8.7 mm larva. The full complements of 16 to 17 anal and 13 to 14 dorsal rays are ossifying in larvae 10.5 mm and larger. In both the anal and dorsal fins, the rays ossify posteriad and anteriad from the more central rays. In both fins the last ray to form is the short anteriormost ray.

Pelvic fin buds appear at about 6.2 mm length, but, the rays do not begin to ossify until the larvae reach about 9 mm. The full complement of 8 pelvic rays is ossifying in larvae 11.8 mm and larger.

Pigmentation.—Preflexion larvae (3.8 to ca. 6.0 mm) have two pairs of pigment dashes developed on the gut. The anterior pair is on the foregut posterior to the cleithra, while the posterior pair is on the free terminal section of the gut. The most conspicuous pigment in preflexion larvae is the series of four to eight melanistic spots or dashes on the ventral midline of the tail. By the end of the preflexion stage, melanistic pigment is developing over the gas bladder. Also the anterior foregut spots have coalesced and moved forward and dorsad to form a pigment shield over the anterior part of the liver.

Flexion larvae (6.2 to ca. 7.5 mm) have essentially the same pigment as in preflexion larvae. The ventral tail spots range from three to seven (mean of 4.4 for 27 specimens). The median ventral foregut pigment spot or patch is continuously present as are the paired patches or streaks of pigment on the free terminal section of the gut. Pigment above the gas bladder increases in amount, with sometimes a pair of internal pigment spots located between the gas bladder and the termination of the gut.

A single pigment spot develops over the hind brain in some specimens; of the 27 specimens between 6.2 to 7.5 mm, only four had this head pigment spot. Two specimens in this size range, 6.5 and 7.2 mm respectively, had a double row of small dorsal pigment spots (seven to eight spots per side) extending for most of the length of the tail portion of the body.

In postflexion larvae (7.7 to 13.9 mm) the pigment areas already described either persist or are more consistently present, and additional pigment develops on the head, back, and in the caudal region. The pigment over the gas bladder increases in extent and begins to spread laterally. Melanistic pigment is present on the cleithral margin forward of the pectoral base on most larvae 9.2 mm and larger. The ventral midline of pigment spots becomes imbedded and sometimes faint, but was absent on only four specimens. The number of pigment spots ranges between two and five (mean of 3.6 spots on 43 specimens). The imbedded pigment spot on the hind brain occurs on about ⅓ of the larvae between 7.7 and 8.7 mm, but thereafter is consistently present. By about 10 mm, two spots form over the cerebellum and are usually present on larvae larger than this. The double row of dorsal tail pigment spots is only sporadically present on larvae under 10.5 mm, but consistently present on larger larvae. The rows extend from about the termination of the dorsal fin, almost to the procurrent caudal rays; the usual count is seven or eight spots per side, but the range is from two to thirteen spots. Internal pigment forms over the hypurals, usually adjacent to the ural centrum; this pigment, first observed on a 7.7 mm specimen, is infrequently present on larvae under 10.5 mm. Pigment also forms at the hypural edge of the caudal fin. It was first observed on a 7.2 mm larva and was sporadically present until 10.5 mm. On older specimens this pigment becomes almost continuous along the hypural edge. The 14.9 mm transforming specimen added a line of dorsal pigment spots to the nape and trunk; however, a 14.2 mm juvenile had pigment over the entire body and the peritoneum was conspicuously black.

Photophore development.—A number of photophores form on larvae of *Lampanyctodes* prior to transformation. As is usual in myctophids, the Br_2 pair is the first to form; it was consistently present on specimens 6.6 mm and larger. The Vn, the second pair to form, was first observed on a 7.5 mm specimen and was consistently present by 7.8 mm. The third pair, PO_5, was present by 8.7 mm. A specimen 11.2 mm had two additional pairs, the PLO and PO_1; however, specimens 11.7 and 11.8 mm had added only the PLO pair, indicative that it forms somewhat sooner than the PO_1. Specimens 12.0 mm and larger consistently had both these pairs. A 12.7 mm specimen had three additional pairs faintly formed, the VLO, OP_2, and PO_2; however, none of these was present on a 13.7 mm specimen, and only the VLO pair was present on a 13.8 mm and a 14.4 mm specimen. A transforming specimen 14.9 mm long had the majority of photophores formed. The initial five pairs to form, the Br_2, Vn, PO_5, PLO and PO_1 became conspicuous photophores soon after their formation. This was not the case for the three other pairs

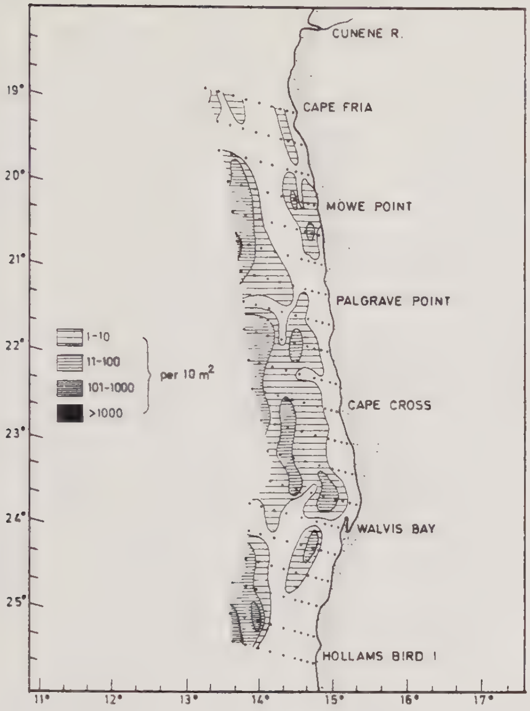
CUNENE R.
CAPE FRIA
MÖWE POINT
PALGRAVE POINT
CAPE CROSS
WALVIS BAY
HOLLAMS BIRD I
1-10
11-100
101-1000
>1000
per 10 m²
19°
20°
21°
22°
23°
24°
25°
11°
12°
13°
14°
15°
16°
17°

Figure 5. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 1 (August 1972 to March 1973). Numbers represent cumulative standard haul totals.

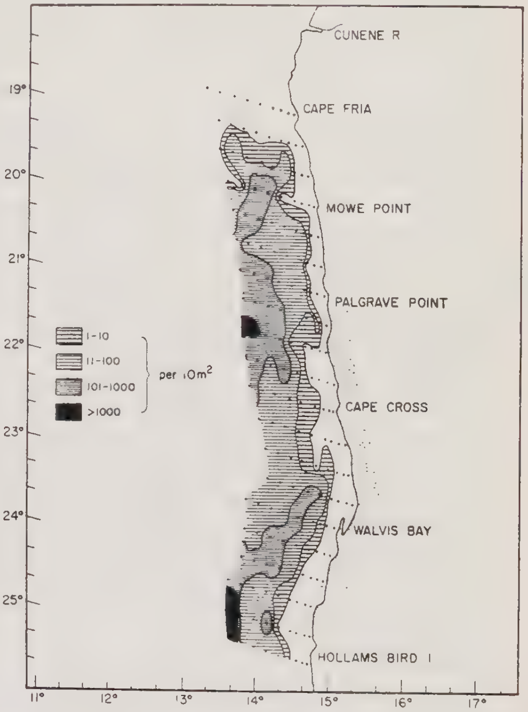
CUNENE R
CAPE FRIA
MOWE POINT
PALGRAVE POINT
CAPE CROSS
WALVIS BAY
HOLLAMS BIRD I
1-10
11-100
101-1000
>1000
per 10m²
19°
20°
21°
22°
23°
24°
25°
11°
12°
13°
14°
15°
16°
17°

Figure 6. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 2 (August 1973 to April 1974).

mentioned above which, at best, were but faintly developed on late-stage larvae prior to transformation.

DISTRIBUTION

Lampanyctodes hectoris is a neritic species associated with land masses in the vicinity of the subtropical convergence. It is known from South Africa, New Zealand, Southern Australia, and Chile, but apparently does not occur in the western Atlantic off Argentina (McGinnis, 1974). Where it occurs, it is highly abundant, as demonstrated by the fishery off South Africa. It may occur in commercial abundance in other southern ocean areas.

There are no available data on the distribution and abundance of the larvae in the area of the fishery off South Africa, but SWAPELS provides larval data from an area just to the north of the fishery. Results from the two year survey show that larvae of the family Myctophidae formed 9.75 percent of all the fish larvae taken and larvae of *L. hectoris* comprised over 85 percent of all myctophid larvae. This species was widely distributed between latitudes 19° and 25° S (Figs. 5 and 6). Larvae were found at distances of 8 to 112 km from the coast but were most abundant in offshore waters especially between Möwe Point (20°20′ S) and Cape Cross (22° S) and between Walvis Bay (23° S) and Hollams Bird Island (25° S). Approximately 93 percent of all larvae were taken during the months of August, September, October, and November of both years. Early larval stages (those less than 5.0 mm in length) were common from August to October, but were most abundant in the plankton in August particularly in the region west of Hollams Bird Island. Over 62 percent of all early larval stages were taken during this month. The larvae of *L. hectoris* were found at surface temperatures ranging from 13.9° to 21.5° C. However, over 60 percent of all larvae occurred at mean surface temperatures of 14.0° to 15.5° C.

SYSTEMATIC RELATIONSHIPS

Although the photophores of *L. hectoris* were not mentioned in the original description of the species

(Günther, 1876), Fraser-Brunner (1949) was well aware of the unique arrangement of the light organs and, accordingly, created the genus *Lampanyctodes* for this species. He noted the marked ventral placement of the two longitudinal series of photophores, a feature which he thought was more characteristic of the "primitive" myctophine lanternfishes than of the lampanyctine genera to which it was obviously allied on the basis of morphological characters. He mentioned particularly the horizontal positioning of the two PVO photophores, an arrangement found only in the myctophine genera *Protomyctophum*, *Diogenichthys*, and *Benthosema*. His view of *Lampanyctodes* as a primitive lampanyctine genus is demonstrated by the statement, "this genus is clearly indicative of the form from which *Lampanyctus*, *Gymnoscopelus* and their allies have been derived." He did not elaborate on the relationships of *Lampanyctodes* with other lampanyctine genera nor did he construct a higher classification for lanternfishes.

It remained for Paxton (1972) to formally recognize the two subfamilies Myctophinae and Lampanyctinae and to construct a higher classification that included six tribes, two in the Myctophinae and four in the Lampanyctinae. In the latter subfamily he recognized the monotypic tribe Notolychnini, the tribe Lampanyctini consisting of eight genera, Diaphini with two genera, and Gymnoscopelini with eight genera. *Lampanyctodes* was important in his tribal arrangement as shown by his statement "the Diaphini and Gymnoscopelini are closely related, for the most primitive genus of each group, *Lobianchia* of the Diaphini and *Lampanyctodes* of the Gymnoscopelini, share a number of characters. Each form has widely ossified pubic plates, a relatively low number of ventral procurrent rays, well-developed caudal glands, one or two elevated PO photophores, and an arched or elevated series of VO photophores . . . ." He viewed *Lampanyctodes* as an essentially intermediate form that branched from the main line of gymnoscopeline evolution soon after the divergence of this tribe from the Diaphini.

Using the combination of larval and adult characters, Moser and Ahlstrom (1972) proposed a phylogenetic scheme for the subfamily Lampanyctinae that recognized the four tribes of Paxton (1972) but differed in the placement of certain genera in the Lampanyctini and Gymnoscopelini. We believe that the triad of genera, *Bolinichthys*, *Ceratoscopelus* and *Lepidophanes* belong in the Gymnoscopelini whereas Paxton placed them in the Lampanyctini. Also, we would include two other of Paxton's lampanyctine genera, *Lampadena* and *Taaningichthys*, in the Gymnoscopelini. These form a triad with the recently described *Dorsadena*. Our conception of tribal and generic relationships in the subfamily Lampanyctinae based on a combination of larval and adult characters is shown in the dendrogram (Fig. 7). Essentially the tribe Gymnoscopelini consists of the two above mentioned triads, the triad of *Lampichthys*, *Notoscopelus* and *Scopelopsis*, the well differentiated genus *Gymnoscopelus* and two monotypic isolated genera, *Hintonia* and *Lampanyctodes*. Based on Paxton's adult characters, and the larval characters given below and in Moser and Ahlstrom (1972), the genus *Gymnoscopelus* ~~is~~ closest to the Diaphini and in a direct line from the original tribal split. We have not yet identified the larvae of *Hintonia* and accept the view of Paxton that the genus has no distinct relationship to any member of the tribe and that this form split off early from the ancestral stock.

The genus *Lampanyctodes* is the most problematic and, phylogenetically, the most intriguing genus in the tribe. Its photophore arrangement is so unusual that it warrants a brief review. All photophores are relatively low on the body, including the PLO, VLO, 3rd SAO, POL and terminal Prc, all of which are well below the lateral line. Both a Dn and Vn pair of eye photophores are formed, although the Dn develops quite late. This feature is shared with *Lampichthys*, *Scopelopsis*, *Notoscopelus*, *Hintonia*, *Diaphus* (usually) and *Gymnoscopelus* among the Lampanyctinae and with most genera of Myctophinae.

Of particular interest is the horizontal arrangement of the two PVO photophores, an arrangement not found in any other genus of the Lampanyctinae, but present in three myctophine genera, as previously noted.

Although *Lampanyctodes* has the usual number of PO photophores, five, it is unique in having the PO_3 elevated rather than the PO_4. *Lampanyctodes* also has the usual number of VO photophores for Lampanyctinae, five, but has the series evenly arched, an unusual arrangement also found in some *Lampanyctus*. None of the AO series is elevated, the usual arrangement in most kinds of lanternfishes. The presence of a single POL is shared with all genera of *Myctophinae* except *Hygophum*, and with a half dozen genera of Lampanyctinae (*Diaphus*, *Lobianchia*, *Taaningichthys*, *Lampadena*, *Gymnoscopelus* and *Steno-*

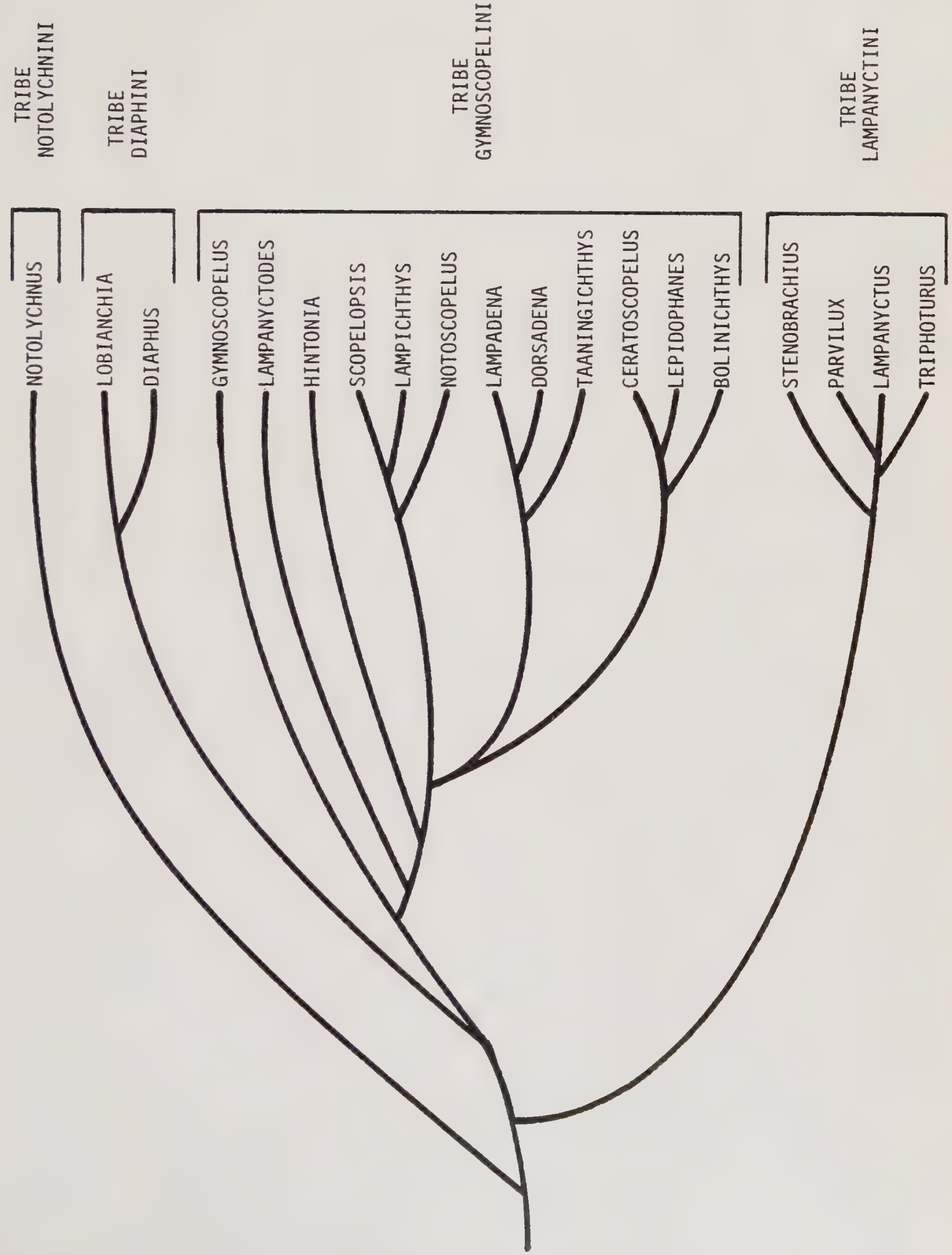
TRIBE NOTOLYCHNINI
TRIBE DIAPHINI
TRIBE GYMNOSCOPELINI
TRIBE LAMPANYCTINI
NOTOLYCHNUS
LOBIANCHIA
DIAPHUS
GYMNOSCOPELUS
LAMPANYCTODES
HINTONIA
SCOPELOPSIS
LAMPICHTHYS
NOTOSCOPELUS
LAMPADENA
DORSADENA
TAANINGICHTHYS
CERATOSCOPELUS
LEPIDOPHANES
BOLINICHTHYS
STENOBRACHIUS
PARVILUX
LAMPANYCTUS
TRIPHOTURUS

Figure 7. Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae based on a combination of larval and adult characters.

TABLE 3. Size at formation and sequence of early forming photophores for 10 genera of *Lampanyctinae*.

	Size at transformation (mm)	Br_2	Vn	PO_5	PLO	PO_1
Lampanyctodes hectoris	14–15	6.6 (1)	7.8 (2)	8.7 (3)	11.7 (4)	Ca 12.0 (5)
Ceratoscopelus townsendi	16.5–18	7.0 (1)	7.8 (2)	9.0 (4)	8.7 (3)	–
Lepidophanes guentheri	–	<9.5	<9.5	<9.5	<9.5	–
Notoscopelus resplendens	19–21	4.2 (1)	9.2 (3)	6.2 (2)	Ca 15.0 (4)	–
Lampichthys rectangularis	19–21	<7.0 (1)	9.8 (3)	8.4 (2)	Ca 16.0 (4)	16.4 (5)
Lampadena urophaos	17–21	6.2 (1)	13.4 (4–5)	9.8 (3)	7.3 (2)	13.4 (4–5)
Scopelopsis multipunctatus	16.5–17.5	5.4 (1)	11.3 (3)	10.8 (2)	–	–
Gymnoscopelus aphya	Ca 30	<23.5 (1)	–	<23.5 (2–3)	–	<23.5 (2–3)
Diaphus theta	10–11	6.0 (1)	–	6.2 (2)	–	7.6 (3)
Lobianchia gemellari	–	5.5 (1)	–	7.0 (3)	–	6.2 (2)

brachius). The possession of five Prc's is unusual, as is their arrangement in an ascending line that terminates well below the lateral line.

Lampanyctodes is among the genera that develops accessory patches of luminous tissue on the body, a character shared with most members of the tribe *Gymnoscopelini*, as we interpret it, and with *Diaphus* (most species) and *Lampanyctus* (some species). None of the myctophine genera develops accessory luminous tissue other than the supra and infracaudal glands. In *Lampanyctodes* the luminous tissue develops at the bases of the dorsal, anal, pectoral and pelvic fins, before and behind the dorsal fin, and on the dorsal surface of head; this pattern is suggestive of that developed on *Ceratoscopelus* and *Bolinichthys*. No secondary photophores are developed.

The fact that, in its arrangement of light organs, *Lampanyctodes* shares so many characters with so many other genera of Lampanytinae, and even shares a fundamental character (the horizontal PVO's) with some genera of the Myctophinae has produced an understandable confusion as to the position of this genus. We would agree with Fraser-Brunner (1949) and Paxton (1972) that the genus has had a long and independent evolution but do not consider it a primitive genus. We believe it is a highly specialized form and that the ventral and basically linear placement of photophores is related to its mode of life in shallow neritic waters. Our thesis that the arrangement of ventrally placed, well developed linear series of photophores, such as is found in most Myctophinae, is an adaptation for countershading in shallow-living lanternfishes has been stated in detail in previous papers (Moser and Ahlstrom, 1972, 1974).

The relationships of *Lampanyctodes* to other genera of Gymnoscopelini is seen more clearly from an examination of larval characters. It develops the dorsal series of pigment spots found in so many members of this tribe and, more importantly, forms several of the same photophores during the larval period (Table 3).

In an attempt to analyze the position of *Lampanyctodes* in the subfamily Lampanyctinae we selected 10 larval characters and 10 adult characters of this genus and compared them with all other genera in the subfamily. *Dorsadena* and *Hintonia* were excluded since their larvae are unknown. Two groups of larval characters were selected, those related to early forming photophores, and those related to pigment patterns. Adult characters were based mostly on photophore arrangements, presence or absence of luminous caudal glands, accessory luminous tissue, secondary photophores, sexual dimorphism, keel or ridge on fifth circumorbital bone, and a supra-

TABLE 4. Larval and adult characters of *Lampanyctodes hectoris* compared with other genera of the subfamily *Lampanyctinae*.

	Lampanyctodes	*Lampichthys*	*Scopelopsis*	*Notoscopelus*	*Ceratoscopelus*	*Lepidophanes*	*Bolinichthys*	*Lampadena*	*Taaningichthys*	*Gymnoscopelus*	*Diaphus*	*Lobianchia*	*Lampanyctus*	*Triphoturus*	*Stenobrachius*	*Parvilux*	*Notolychnus*
Larval characters																	
Early forming photophores																	
Br_2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−
Vn	+	+	+	+	+	+	−	+	−	−	−	−	−	−	−	−	−
PO_5	+	+	+	+	+	+	−	+	−	+	+	+	−	−	−	−	−
PLO	+	+	−	+	+	+	−	+	−	−	−	−	−	−	−	−	−
PO_1	+	+	−	−	−	−	−	+	−	+	+	+	−	−	−	−	−
Pigment characters																	
Series of ventral pigment spots (preflexion)	+	+	+	−	+	+	+	−	−	+	+	−	− +	+	+	?	+
Ventral series retained (postflexion)	+	+	+	−	−	−	−	−	−	+	+ −	−	−	−	−	−	−
Pigment back of head	+	+	+	+	+ −	+	+	+	+	+	− +	−	+ −	−	+ late	+	−
Dorsal body pigment	+	+	+	+	+ −	+	+ −	+	+	+	−	−	− +	+	+ late	+	−
Caudal pigment	+	+	+	+	−	−	−	−	+	+	+ −	+ −	−	−	−	−	+
Adult characters																	
Supramaxillary present	+	+	+	+	−	−	−	−	−	+	−	−	−	−	−	−	−
Circumorbital 5 keel or ridge	+	+	+	+	−	−	−	−	−	+	+ −	+	−	−	−	−	?
One or more VO's elevated	+	−	−	−	+	+	+	−	−	−	+	+	+ −	+	−	−	+
Single POL	+	−	−	−	−	−	−	+	+	−	+	+	−	−	+	−	−
Dn and Vn development	+	+	+	+	−	−	−	−	−	+	+ −	−	−	−	−	−	−
Supracaudal glands developed	+	+	+	+ −	+	+	+	+	+	−	−	+	+	+	+	+	+
Infracaudal glands developed	+	+	−	−	+	+	+	+	+	−	−	+	+	+	+	+	−
Accessory luminous tissue	+	+	+	+	+	+	+	−	−	+	+ −	−	+ −	−	−	−	−
Sexual dimorphism lacking	+	+	−	−	−	?	−	+	−	−	−	−	+	+	+	+	−
Secondary photophores lacking	+	−	−	+	+	−	−	+	+	+	+	+	+ −	+	+	+	+

maxillary. Presence of a character was rated as a "plus" and absence as a "dash". Because of variability occurring among species in some genera, some characters had to be rated both "plus" and "dash" (Table 4). In making a summation, characters rated as both "plus" and "dash" were weighted ½.

We do not assume that these 20 characters are of equal phylogenetic importance, even though none is trivial. We selected characters that are present or absent, hence had to ignore equally relevant characters that can not be so rated. Among the adult characters chosen, luminous glands on the caudal peduncle (supra and infra) probably are the most problematical, in that their presence or absence may not be as important phylogenetically as are the structural and functional differences in these glands among genera. These differences cannot be simply rated by this technique.

As noted earlier, the initial five pairs of photophores to develop on *Lampanyctodes* during the larval period are Br_2, Vn, PO_5, PLO, and PO_1. As indicated in table 4, all five pairs are also developed on *Lampichthys* and *Lampadena*, although not in the same sequence as in *Lampanyctodes*. Four of the above pairs are early forming on *Notoscopelus*, *Ceratoscopelus*, and *Lepidophanes*, three of the above pairs in *Scopelopsis*, *Gymnoscopelus*, *Diaphus* and *Lobianchia* and the remaining seven genera lack early forming photophores other than the Br_2 pair. We consider the striking similarity of these early forming pairs among genera as evidence of close relationship.

The other characters selected for larvae involve pigment patterns, including the presence or absence of a row of ventral midline pigment spots on the tail of preflexion and late-stage larvae, and the development of pigment on the back of the head, along the dorsal margin of the body, or at the base of the caudal fin of postflexion larvae.

Certain relationships emerge when the characters in the table are summed. *Lampanyctodes* is found to be most closely related to *Lampichthys* (17 points), then to *Scopelopsis* (13), *Gymnoscopelus* (13), *Notoscopelus* (12½), *Lampadena* (12), *Ceratoscopelus* (11), and *Lepidophanes* (11). These genera are among those we place in the tribe Gymnoscopelini. Although it is true that larval characters strongly influence this rating, so do several of the adult characters, such as the presence of a supramaxillary, Dn and Vn photophores, and accessory luminous tissue. *Lampanyctodes* is close to three genera that Paxton (1972) and Moser and Ahlstrom (1972) have previously shown to be closely allied (*Lampichthys, Scopelopsis*, and *Notoscopelus*), but also to *Gymnoscopelus*, and must have split off from the ancestral line of the triad soon after it diverged from the *Gymnoscopelus* line.

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REPORT OF NEUSTON (SURFACE) COLLECTIONS MADE ON AN EXTENDED CalCOFI CRUISE DURING MAY 1972

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ABSTRACT

This is the first report on neuston samples collected during CalCOFI cruises. Fortunately, Cruise 7205 covered an extensive area of the temperate north Pacific.

Some fish spend their young stages in surface waters or migrate into this zone diurnally, particularly at night. For these the neuston collections provide insights that cannot be observed in the standard oblique plankton collections. The neuston net samples some species in far greater numbers—the Pacific saury is a prime example—and so is an excellent tool for establishing distribution and relative abundances. The neuston net samples a higher proportion of large larvae of some species, the northern anchovy for example, than does the oblique net, and so may become a valuable tool in mortality determinations. Other genera in which the neuston net sampled larger larvae than are usually taken in the oblique net include *Sebastes, Anoplopoma,* and *Macrorhamphosus.* The neuston collections of oceanic fishes in the family Myctophidae demonstrate interesting behavioral pattern differences between its two subfamilies. In one subfamily, Myctophinae, only juveniles and adults were taken. In the subfamily Lampanyctinae only larvae were taken. This marked contrast in behavioral pattern of the two subfamilies is not evident in oblique hauls.

The comparison of the neuston and oblique plankton collections shows the neuston net to be a highly selective gear, sampling some species in much greater abundance than the oblique net but also sampling far fewer species than the oblique plankton net. The neuston net presents interesting potentialities when used in addition to the standard oblique net.

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INTRODUCTION

This is the first report on neuston net collections made on cruises of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). The collections were taken on extended Cruise 7205 which covered the cardinal lines of the regular CalCOFI pattern from line 10 off Puget Sound to Line 150 off southern Baja California as well as the terminal line, line 157 below Cape San Lucas, Baja California, a north-south extent of 1,680 miles (48° to 20° N). In addition, extensive offshore coverage was achieved by adding eight lines of offshore stations west of the CalCOFI pattern along latitudes 20°, 24°, 27°, 31°, 35°, 39°, 42°, and 46° N, extending offshore usually to 145° W longitude (Figure 1). This coverage is almost as extensive as that obtained by CalCOFI vessels on the cooperative NORPAC Expedition of 1955. A total of 105 neuston hauls was obtained over the regular CalCOFI grid and 43 hauls on the eight offshore lines.

METHODS AND EQUIPMENT

The neuston net hauls were made simultaneously with the oblique plankton tows. This was achieved by launching the neuston net from a different winch located on the opposite side of the vessel simultaneously with the launching of the net assembly for the oblique hauls; it was retrieved at the same instant as the oblique tow. Speed of hauling was 1.5 to 2 knots. The duration of the haul averaged 21.5 minutes. Inasmuch as we wish to compare the catches made by the two types of hauls, neuston versus oblique, only those stations are included where both types of catches were made.

The neuston net used on this CalCOFI cruise was anything but sophisticated. A CalCOFI meter net frame (1.0 m diameter) was bent from round to ovoid, and a styrofoam float was fastened in either side of the mouth of the net. The floats maintained the net so that only about half of the mouth was under water. A standard CalCOFI net constructed of 505 micron mesh was utilized. It is estimated that the effective straining area at the mouth was about 0.3 m^2. As might be anticipated, the net performed consistently well in relatively calm seas, and less so in

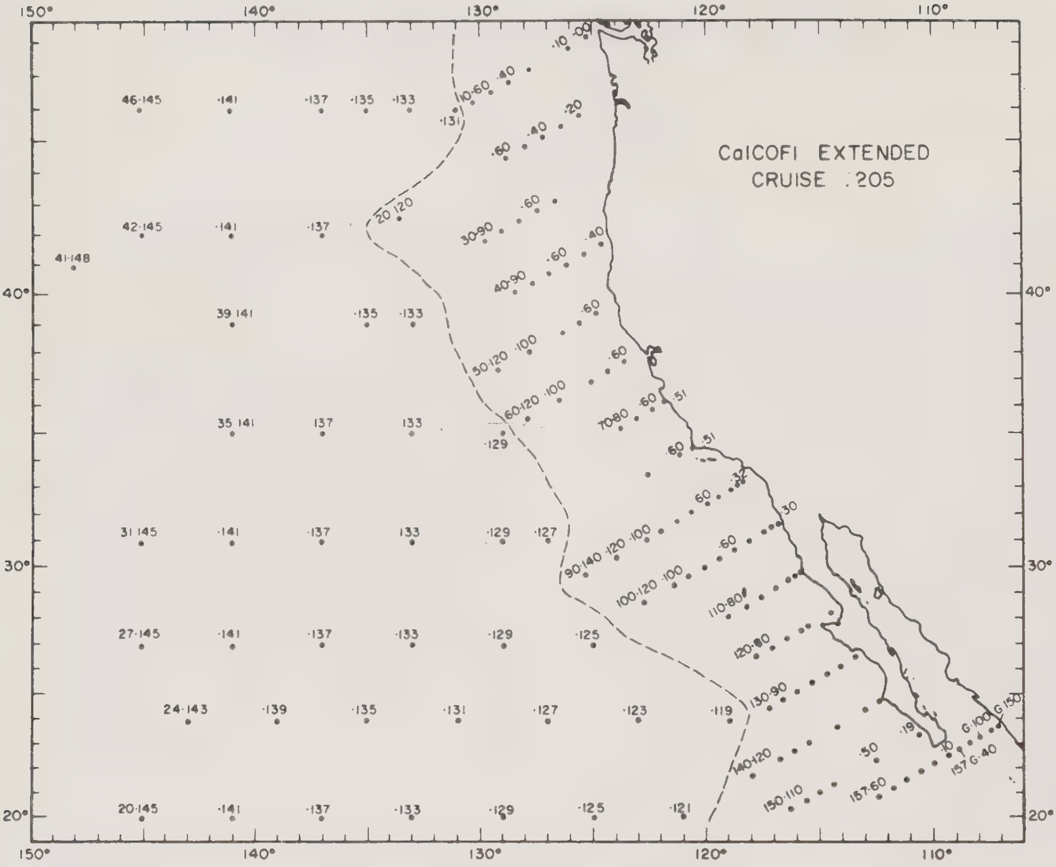
CalCOFI EXTENDED
CRUISE 7205
150°
140°
130°
120°
110°
40°
30°
20°
46·145
42·145
41·148
39·141
35·141
31·145
27·145
24·143
20·145
10·60
20·120
30·90
40·90
50·120
60·120
70·80
90·140
100·120
110·80
120·80
130·90
140·120
150·110
157·60
G·100
G·150
157 G·40

FIGURE 1. Station pattern for CalCOFI extended Cruise 7205.

more turbulent seas. The amount of water strained by the neuston net in moderate seas is estimated to be between 250 to 300 m^3. No current meter was used in the neuston net; however, a current meter was used in taking the simultaneous oblique haul, also utilizing a 505 micron mesh CalCOFI net. Information on distance traversed during each haul can be derived from this current meter's readings. The regular CalCOFI net was lowered to about 200 m depth (300 m of wire payed out) and retrieved at a uniform rate.

The regular CalCOFI cruises do not extend far enough offshore to completely delimit the spawning distribution of jack mackerel, *Trachurus symmetricus*, or of the Pacific saury, *Cololabis saira*. Eggs and larvae of these two species usually are at or near their peak abundance during May. Cruise 7205 was designed, in part, to more effectively sample the offshore distributions of these two species. As our results will demonstrate, the neuston net is a much more effective gear for sampling the larvae and juveniles of the Pacific saury than is our CalCOFI gear. Although both nets sampled eggs and larvae of jack mackerel, the CalCOFI oblique hauls obtained these in more collections.

RESULTS

Number of Specimens Taken

In the following discussion and throughout this presentation, we are dealing with actual counts of specimens taken in hauls. No attempt has been made to standardize the counts since there is no simple way to standardize counts from neuston hauls.

The number of fish larvae per collection in the neuston net ranged from zero to 1,039. Numbers of specimens per haul were grouped in six categories of abundance for both neuston and oblique hauls

TABLE 1

Summary for Six Abundance Categories of Number of Larvae per Collection for Neuston Hauls and Oblique CalCOFI Net Hauls on Extended CalCOFI Cruise 7205

Lines	Neuston net collections								Oblique net collections							
	Number larvae per haul								Number larvae per haul							
	0	1-10	11-50	51-100	101-1,000	over 1,000	Total	Average no/station	0	1-10	11-50	51-100	101-1,000	over 1,000	Total	Average no/station
Regular CalCOFI pattern																
10- 50	11	12	1	3	1	0	28	31.2	2	8	15	3	0	0	28	21.8
60-100	3	14	9	3	4	0	33	75.6	0	4	11	4	12	2	33	248.8
110-150	1	13	13	2	3	1	33	58.8	0	4	10	4	13	2	33	215.4
157	1	1	2	2	5	0	11	156.6	0	0	2	1	8	0	11	354.5
Subtotal	16	40	25	10	13	1	105	67.0	2	16	38	12	33	4	105	188.8
Offshore latitudinal lines																
46- 41	6	3	1	0	0	0	10	2.2	0	1	9	0	0	0	10	26.6
39- 31	2	3	5	2	1	0	13	33.4	0	1	3	3	6	0	13	78.5
27- 20	0	4	12	4	0	0	20	28.6	0	0	4	6	10	0	20	130.6
Subtotal	8	10	18	6	1	0	43	23.9	0	2	16	9	16	0	43	90.7
Total	24	50	43	16	14	1	148		2	18	54	21	49	4	148	
% of total whole numbers	16	34	29	11	9	1	100		1	12	37	14	33	3		

(Table 1). Fewer larvae were taken on the average in neuston hauls. Samples having zero to 10 larvae made up fully 50%; with zero hauls contributing 16%, hauls with one to 10 larvae, 34%. The contributions of other abundance categories was as follows: samples with 11 to 50 specimens, 29%, samples with 51 to 100 specimens, 11%, and samples with 101 or more, 10%.

In the oblique hauls, 50% had 50 or fewer larvae; with two zero hauls contributing slightly more than 1%, hauls with one to 10 larvae comprising 12% and hauls with 11 to 50 larvae, 37%. One-half of the oblique hauls contained 51 or more larvae, with 3% containing over 1,000 larvae, 33% with 101 to 1,000 larvae, and 14% with 51 to 100 larvae.

Fewer larvae were taken in the northern part of the survey area than elsewhere by both types of plankton hauls. Thus, on the upper five lines (10 to 50) of the regular CalCOFI grid, an average of only 22 larvae per haul was obtained in oblique hauls, whereas an average of fully 10 times as many larvae per haul was obtained from the remainder of the CalCOFI pattern.

The contrast in numbers between the two types of hauls was most pronounced on the two northern offshore latitudinal lines (along latitude 46° and 41°) where only 2.2 specimens per haul were taken by the neuston net as compared to 26.6 specimens per haul in oblique collections. Over the regular CalCOFI pattern, the average catch in the neuston hauls was approximately one-third that taken in oblique hauls, and was somewhat less than one-third in offshore stations.

Kinds of Larvae Taken

Regular CalCOFI Stations (Lines 10 to 157)

Neuston net hauls. The neuston net at stations of the regular CalCOFI grid caught 7,031 larvae-juveniles belonging to 51 categories (Table 2). Of these, two were Clupeiformes, three Stomiatoidei, 10 Myctophidae, three Scomberesocidae-Exocoetidae, six Scorpaeniformes, four Pleuronectiformes, 16 Perciformes, and seven others. Absent from the neuston collections were larvae of Argentinoidei, Myctophiformes other than Myctophidae, and Melamphaidae. Taken exclusively in the neuston hauls were larvae- juveniles of *Anoplopoma fimbria* (468 specimens in seven hauls), *Macrorhamphosus gracilis* (43 specimens in seven hauls), and *Opisthonema* sp. (149 larvae in three hauls). The average number of larvae per haul was 67.0.

In the neuston hauls 10 categories (six species, four genera) contributed 91.4% of the total, as follows: *Engraulis mordax*, 43.3%; *Cololabis saira*, 15.6%; *Oxyporhampus micropterus*, 11.2%; *Anoplopoma fimbria*, 6.7%; *Tarletonbeania crenularis*, 4.2%; *Oligoplites* sp. 3.6%; *Opisthonema* sp., 2.1%; *Sebastes* sp., 1.9%; *Vinciguerria lucetia*, 1.9%, and *Auxis* sp., 0.9%.

Oblique net hauls. Almost 2.5 times as many kinds of larvae were taken in the oblique hauls as in neuston hauls made over the regular CalCOFI grid of stations; 123 categories as compared to 51 (Table 2). The breakdown of the kinds of larvae taken in regular hauls was as follows: two Clupeiformes, 10 Argentinoidei, 10 Stomiatoidei, 26 Myctophidae, 12 other Myctophiformes, five Anguilliformes, three Scomberesocidae-Exocoetidae, five Gadiformes, three Melamphaidae, 12 Pleuronectiformes, seven Scorpaeniformes, 22 Perciformes, and six others. The average number of larvae per haul was 188.8.

In the oblique hauls, 10 categories (eight species, two genera) contributed 87.1% of the larvae obtained, as follows: *Engraulis mordax*, 53.8%;

TABLE 2

Comparisons of Catches of Neuston Net and Oblique CalCOFI Net at 105 Stations Over the Regular CalCOFI Pattern on Cruise 7205

	Neuston				Oblique			
	Occurrences	Number Specimens	Stage	Size Range (mm)	Occurrences	Number Specimens	Stage	Size Range (mm)
Clupeidae:								
Opisthonema sp.	3	149	L	3.0–15.0	0	0	--	0
Engraulidae:								
Engraulis mordax	25	3,041	L	2.5–31.0	36	10,671	L	2.0–20.5
Bathylagidae:								
Leuroglossus stilbius	0	0	--	--	20	128	L-J	2.3–19.0
Bathylagus nigrigenys	0	0	--	--	8	45	L	2.5–10.0
Bathylagus ochotensis	0	0	--	--	25	70	L-J	4.9–27.5
Bathylagus wesethi	0	0	--	--	15	189	L	2.5–18.0
Sternoptychidae:								
Cyclothone spp.	0	0	--	--	12	68	L	3.3–13.5
Vinciguerria lucetia	7	136	L	2.0–15.5	35	3,162	L	2.0–19.0
Myctophidae:								
Ceratoscopelus townsendi	0	0	--	--	10	90	L	2.0–12.0
Diaphus spp.	2	4	~~L~~	4.2– 5.2	14	79	L	2.5– 6.6
		1	L	3.8				
Diogenichthys laternatus	2	1	J-A	19.5	7	673	L	1.8–10.4
Gonichthys tenuiculum	11	41	J-A	14.5–57.5	9	48	L	2.0– 6.7
Hygophum atratum	4	50	J-A	14.5–57.5	16	123	L	1.8–13.5
Lampadena urophaos	2	17	L	5.0– 6.5	4	18	L	2.9– 8.9
Lampanyctus spp.	1	2	L	3.4, 4.0	60	222	L	2.0–14.0
Myctophum nitidulum	1	1	J-A	35.0	1	1	L	4.0
Protomyctophum crockeri	0	0	--	--	40	102	L	2.5–19.0
Stenobrachius leucopsarus	3	4	L	3.5–13.2	40	277	L	2.5–14.0
Symbolophorus californiensis	3	3	J-A	39.5–71.0	14	81	L	2.9–12.5
Tarletonbeania crenularis	12	296	J-A	20.5–67.0	31	130	L	3.3–18.0
Triphoturus mexicanus	0	0	--	--	37	355	L	1.5– 9.4
Other myctophids incl unident	4	5	--	--	9*	128	--	--
Scomberesocidae:								
Cololabis saira	49	1,095	L-J	5.0–57.0	5	8	L	5.6–14.0
Exocoetidae:								
Oxyporhamphus micropterus	8	785	L	3.5–15.0	3	6	L	4.3– 6.5
Others	12	107	L-J	3.2–20.5	0	0	--	--
Merlucciidae:								
Merluccius productus	2	2	L	4.0, 14.5	15	75	L	2.0–16.5
Bregmacerotidae:								
Bregmaceros bathymaster	1	7	L	2.3– 4.0	6	957	L	2.4–11.5
Melamphaidae:								
Melamphaes spp.	0	0	--	--	22	44	L	2.4–20.5
Macrorhamphosidae:								
Macrorhamphosus gracilis	4	43	L-J	8.0–25.5	0	0	--	--
Sphyraenidae:								
Sphyraena sp.	1	31	L	2.5– 5.0	1	119	L	2.3– 4.9
Polynemidae:								
Polydactylus sp.	1	13	L	4.0–13.5	1	5	L	2.0– 3.0
Mugilidae:								
Mugil sp.	7	53	L-J	3.5–19.0	1	1	L-J	19.0
Carangidae:								
Trachurus symmetricus	5	43	L	2.5– 3.5	20	450	L	1.5–15.0
Oligoplites sp.	1	253	L	3.0– 8.5	1	15	L	2.8– 4.3
Coryphaenidae:								
Coryphaena sp.	3	3	L	4.2–15.0	2	4	L	3.0– 5.2
Scombridae:								
Auxis sp.	3	60	L	2.5–11.0	5	93	L	2.0– 5.9
Blenniidae:								
Hypsoblennius sp.	4	6	L	6.6–12.0	1	1	L	3.4
Scorpaenidae:								
Sebastes spp.	15	137	L-J	3.0–33.5	37	307	L-J	3.1–17.0
Cottidae:								
Scorpaenichthys marmoratus	2	6	L	7.0–11.0	0	0	--	.
Anoplopomatidae:								
Anoplopoma fimbria	7	468	L	9.0–32.5	0	0	--	--
Hexagrammidae:								
Hexagrammos sp.	4	5	L-J	12.0–31.0	0	0	--	--
Oxylebius pictus	2	4	L	2.7– 8.9	0	0	--	--
Pleuronectidae:								
Pleuronichthys sp.	2	3	L	5.8– 9.0	3	3	L	2.0– 7.0
Bothidae:								
Citharichthys sp.	3	3	L	3.2– 5.1	8	36	L	2.5–33.5
Paralichthys californicus	2	2	L	7.8, 7.9	1	5	L	2.2– 2.9
Other identified:	18	102	--	--	89*	640	--	--
Unidentified:	5	36	--	--	--	304	--	--
Disintegrated:	6	13	--	--	--	88	--	.
TOTAL	105	7,031	--	--	105	19,823	--	--

* Indicates number of categories included rather than number of occurrences.

TABLE 3

Comparison of Catches of Neuston Net and Oblique CalCOFI Net at 43 Stations Spaced Along Six Offshore Latitudinal Lines on Cruise 7205.

	Neuston				Oblique			
	Occurrences	Number Specimens	Stage	Size Range (mm)	Occurrences	Number Specimens	Stage	Size Range (mm)
Bathylagidae:								
Bathylagus spp.	0	0	--	--	13	50	L	3.7–18.5
Sternoptychidae:								
Cyclothone spp.	2	3	L	2.0– 6.5	32	232	L	2.0–16.0
Diplophos taenia	1	1	L	6.0	6	8	L	4.8–43.5
Sternoptyx sp.	0	0	--	--	23	157	L	2.1– 9.6
Vinciguerria spp.	3	6	L; J-A	7.0–40.0	27	823	L	2.1–19.5
Other	0	0	--	--	10*	107	--	--
Malacosteidae:								
Aristostomias sp.	3	7	L	17.5–42.0	4	8	L	6.1–27.5
Melanostomiidae:								
Bathophilus sp.	5	7	L	4.0–28.0	5	6	L	4.4–26.0
Eustomias sp.	2	2	L	6.0–16.0	0	0	--	--
Stomiatoidei:								
Other	0	0	--	--	8	91	--	--
Myctophidae:								
Bolinichthys sp.	6	38	L	4.3–12.0	9	22	L	2.7– 8.9
Ceratoscopelus spp.	5	46	L	3.2–15.0	30	567	L	1.8–17.0
Diaphus spp.	1	1	L	3.7	17	54	L	2.3– 9.2
Diogenichthys spp.	0	0	--	--	25	250	L	2.0–11.0
Electrona rissoi	0	0	--	--	12	37	L	2.6– 7.5
Gonichthys tenuiculus	2	5	J-A	23.5–46.0	0	0	--	--
Hygophum spp.	1	6	J-A	13.5–22.0	20	84	L	2.4–11.5
Lampadena urophaos	7	144	L	3.5–17.0	16	63	L	2.2–12.5
Lampanyctus spp.	5	6	L	3.5–13.5	36	238	L	2.0– 8.0
Loweina rara	1	1	J-A	24.0	5	7	L	2.9– 8.6
Myctophum nitidulum	1	1	J-A	20.0	18	41	L	2.3– 9.6
Notolychnus valdiviae	0	0	--	--	19	90	L	2.0– 8.7
Notoscopelus resplendens	0	0	--	--	17	86	L	2.3–15.5
Protomyctophum spp.	0	0	--	--	13	35	L	2.5–17.2
Symbolophorus spp.	0	0	--	--	20	77	L	3.2–15.5
Stenobrachius leucopsarus	2	2	L	3.4, 10.0	8	95	L	3.0– 9.0
Taaningichthys minimus	14	142	L	4.5–20.0	3	3	L	4.7– 9.4
Tarletonbeania crenularis	0	0	--	--	8	29	L	5.0–18.0
Triphoturus spp.	0	0	--	--	9	34	L	2.9–11.6
Other	4	10	L, J	3.0–16.5	9*	78	L	2.5–12.0
Paralepididae:								
Several kinds	0	0	--	--	25	49	L	3.0–45.0
Scopelarchidae								
Scopelarchus spp.	0	0	--	--	12	24	L	3.8–29.0
Scomberesocidae:								
Cololabis saira	25	347	L-J	4.5–71.0	1	1	J-A	82.0
Cololabis adocetus	6	158	L-J	4.6–49.0	0	0	--	--
Exocoetidae								
Several kinds	12	64	L-J	4.0–20.5	0	0	--	--
Bregmacerotidae:								
Bregmaceros spp.	0	0	--	--	12	39	L	1.9–19.2
Melamphaidae:								
Several kinds	0	0	--	--	26	88	L	1.8–17.0
Percichthyidae:								
Howella sp.	0	0	--	--	7	25	L	2.3– 4.1
Bramidae.								
Brama japonica	0	0	--	--	4	9	L	3.0– 6.4
Coryphaenidae:								
Coryphaena sp.	2	2	L	11.0–18.0	1	1	L	4.3
Gempylidae—Trichiuridae:								
Several kinds	0	0	--	--	13	19	L	2.1–17.5
Carangidae:								
Trachurus symmetricus	1	18	L	1.7– 3.5	5	62	L	2.0– 4.5
Naucrates ductor	2	2	L	9.5, 10.5	0	0	--	--
Scorpaenidae:								
Sebastes spp.	1	1	L	12.0	1	4	L	7.0–11.5
Ceratioidei								
Five families	0	0	--	--	5*	10	L	2.2– 5.0
Other identified:	0	0	--	--	20*	44	--	--
Unidentified:	3	3	--	--	27	92	--	--
Disintegrated:	3	4	--	--	21	59	--	--
TOTAL	43	1,027		--	43	3,899		--

* Indicates number of categories included rather than number of occurrences.

Vinciguerria lucetia, 16.0%; *Bregmaceros bathymaster,* 4.8%; *Diogenichthys laternatus,* 3.4%; *Trachurus symmetricus,* 2.3%; *Triphoturus mexicanus,* 1.8%; *Sebastes* spp., 1.5%; *Stenobrachius leucopsarus,* 1.4%; *Lampanyctus* spp., 1.1%; and *Bathylagus wesethi,* 1.0%.

Offshore Latitudinal Lines

Neuston net hauls. In the offshore collections, only 24 kinds of larvae-juveniles were taken in the neuston net hauls (Table 3); of these five were Stomiatoidei, 11 Myctophidae, three Scomberesocidae-Exocoetidae, one Scorpaeniformes (*Sebastes* sp.), and three Perciformes (*Trachurus symmetricus, Naucrates ductor,* and *Coryphaena* sp.). The catches were dominated by larvae-juveniles of Scomberesocidae-Exocoetidae and larvae of Myctophidae, which combined contributed 94.5% of the specimens. Two scomberesocids and four myctophids contributed 85.2% of the total, as follows: *Cololabis saira,* 33.8%; *C. adocetus,* 15.4%; *Lampadena urophaos,* 14.0%; *Taaningichthys minimus,* 13.8%; *Ceratoscopelus* sp. (*townsendi*-complex), 4.5%; and *Bolinichthys* sp., 3.7%. The average number of larvae per haul was 23.9.

Oblique net hauls. Markedly more kinds of fish larvae were taken in the oblique plankton hauls made on the offshore latitudinal lines. They were grouped into 85 categories, of which 16 were Stomiatoidei, five Argentinoidei, 24 Myctophidae, 11 other Myctophiformes, four Melamphaidae, 11 oceanic Perciformes, five Ceratiodei, and nine others. The absence of some of these groups from neuston collections, such as the Argentinoidei was anticipated since the larvae were known to occur in or below the thermocline. However, the complete absence from neuston hauls of all myctophiform groups except Myctophidae was not anticipated. Among the myctophiform groups not sampled by the neuston net are the Paralepididae, Scopelarchidae, Scopelosauridae, and Evermannellidae. In the oblique hauls in the offshore area the Myctophidae contributed 48.5%; the Stomiatoidei, 36.7%; Argentinoidei, 1.4%; other Myctophiformes, 2.2%; Melamphaidae, 2.3%; oceanic Perciformes, 3.2%; and all others, 5.7%. The average number of larvae per haul was 90.7.

SPECIES

Inasmuch as we know a great deal about the kinds of larvae taken in our oblique hauls, and very little about the catches from surface neuston nets, we plan to orientate our discussions to the latter. The species or groups we will discuss in some detail are the following: northern anchovy, *Engraulis mordax,* eggs and larvae; Pacific saury, *Cololabis saira,* eggs and larvae-juveniles; jack mackerel, *Trachurus symmetricus,* eggs and larvae; sablefish, *Anoplopoma fimbria,* larvae; rockfish, *Sebastes* spp., larvae; slender snipefish, *Macrorhamphosus gracilis,* larvae-juveniles; myctophid lanternfishes, larvae-juveniles.

Anchovy (Eggs and Larvae), *Engraulis mordax* Girard

Anchovy eggs were taken in 13 neuston net hauls and in '7 oblique plankton hauls at comparable stations (Figure 2). However, the total number of eggs collected was greater in the neuston hauls; 4,529 as compared to 2,741. Studies on vertical distribution of anchovy eggs (Ahlstrom, 1959; Ahlstrom et al., 1958) indicated a variable depth distribution within the upper mixed layer from haul-to-haul, sometimes with largest concentrations near the surface, sometimes not.

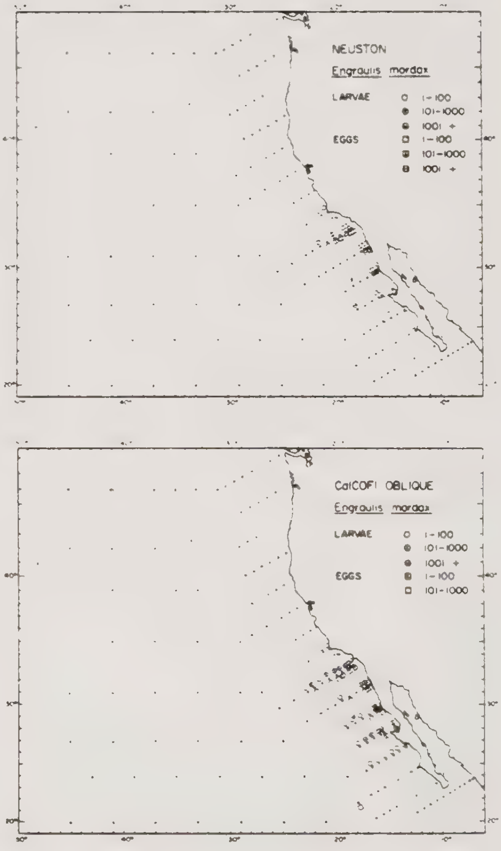

FIGURE 2. Distribution and relative abundance of eggs and larvae of the northern anchovy, *Engraulis mordax,* taken in neuston hauls (upper) and CalCOFI oblique hauls (lower) on Cruise 7205.

We have made two simple assumptions to facilitate comparison of numbers of eggs taken in the two types of hauls, both using 505 micra meshes. First we assumed that the neuston haul strained approximately 30% as much water as the standard oblique haul, and second that anchovy eggs were distributed between the surface and 60 m deep, hence for the oblique hauls which averaged approximately 200 m depth, the net was in water containing anchovy eggs during 30% of the time duration of the haul. If these assumptions are acceptable, the original counts from the two nets should be roughly comparable. The comparisons indicate higher concentrations of eggs near the surface in better than half of the hauls containing 40 or more eggs in either net.

Anchovy larvae were taken in 25 neuston net collections; they were obtained in oblique net hauls made at all of these stations, and at 11 additional stations on which both types of hauls were taken.

As indicated above, it was estimated that the neuston net strained approximately 30% as much water as the obliquely drawn net. The neuston net also collected about 30% as many anchovy larvae as the oblique net. However, anchovy larvae were probably collected during 30% to 50% of the time duration of the oblique haul, because they were seldom deeper than 100 m and usually shallower. Hence, less larvae were taken by the neuston net per unit volume of water strained than by the oblique net while sampling the depth stratum over which anchovy larvae were distributed.

TABLE 4

Extended Cruise 7205, Anchovy Larvae, by Size Category, Taken in Neuston Net Hauls and Regular Plankton Hauls at the Same Stations

Size Category	Neuston	Regular Plankton
2.0	0	88
2.5	1	529
3.0	11	1809
3.5	15	1242
4.0	29	851
4.5	29	598
5.0	41	516
5.5	21	419
6.0	15	437
6.5	32	345
7.0	45	422
7.5	58	349
8.0	131	559
8.5	139	424
9.0	227	402
9.5	171	231
10.0	186	235
10 5	182	152
11.0	182	99
11.5	210	57
12.0	178	39
12.5	159	26
13.0	170	16
13.5	120	12
14.0	118	8
14.5	108	1
15.0	75	5
15.5	67	1
16.0	51	1
16.5	33	
17.25	58	2
18.25	37	1
19.25	27	1
20.25	11	
21.25	5	
22.25	2	
23.25	3	
24.25	4	
..		
28.25	1	
..		
31.25	1	
Dis.	88	788
Total	3,041	10,665

A different segment of the anchovy larvae population was sampled at the surface in neuston net hauls than in the complete depth distribution of anchovy larvae sampled by the oblique plankton hauls (Table 4). Only about 2.5% as many small larvae, 2.0 to 6.0 mm, were taken in neuston hauls as in oblique plankton hauls. Conversely, only 2.5% as many large larvae, 14.5 mm and larger, were taken in the oblique hauls as in the neuston net hauls. These are striking differences. Obviously, larger anchovy larvae tend to congregate in the surface layer. The oblique net collected more larvae of all size categories between 2.0 and 10.0 mm, whereas the neuston net collected more larvae of all size categories, 10.5 mm and longer (Figure 3).

Pacific Saury (Eggs and Larvae), *Cololabis saira* (Brevoort)

The eggs of the Pacific saury are irregularly ovoid in shape, with a cluster of attachment filaments at one pole and a single median filament. The eggs often are found attached to cables or ropes of gear left suspended in the water (i.e. drogues, buoys, nets, etc.). The eggs are sometimes found attached to larger invertebrates, especially salps.

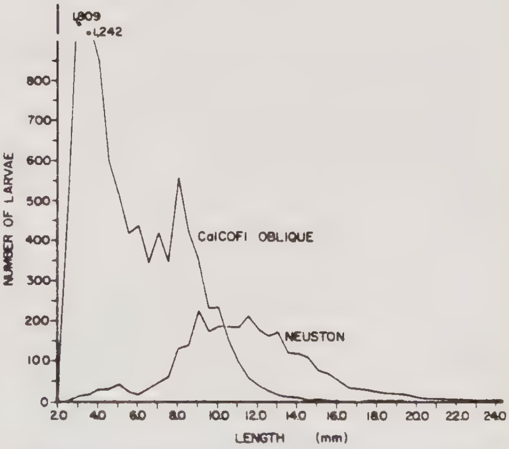

FIGURE 3. Size composition of larvae of northern anchovy, *Engraulis mordax*, in neuston collections versus CalCOFI oblique collections for all stations occupied in Cruise 7205.

The saury egg develops slowly; we lack precise information on rate of development as related to temperature, but it is about 10 days at room temperature for eggs kept in a finger bowl (Smith, Ahlstrom and Casey, 1970).

Despite the fact that saury eggs are spawned in large clusters, the eggs tend to fragment into small clusters (two to 10 eggs) or into individual eggs. Most saury eggs taken in plankton hauls are either individually separate or in small clusters.

Saury eggs were taken in 15 neuston net hauls, all from the regular CalCOFI pattern. Six of the hauls contained a single egg, seven hauls contained two to 10 eggs, one haul had 89 eggs, and one haul contained a very large group of approximately 3,000 eggs. The latter is one of the larger clusters of saury eggs that has been taken in a net haul. Only a single stage of development was observed in the eggs examined from this cluster, and similarly for the sample containing 89 eggs. In two of the samples with small numbers of eggs, two developmental stages were represented, hence these contained eggs spawned on two different nights.

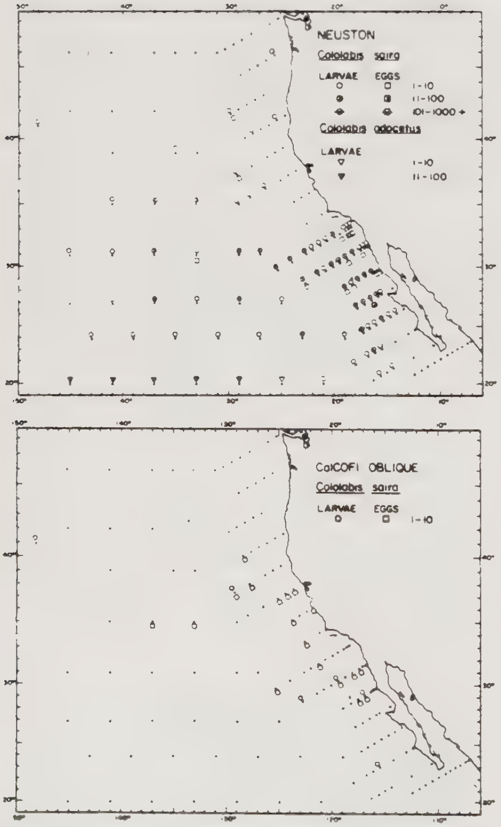

FIGURE 4. Distribution and relative abundance of eggs and larvae of Pacific saury, *Cololabis saira*, taken in neuston hauls (upper) and CalCOFI oblique hauls (lower). Larvae of *Cololabis adocetus* taken only in neuston hauls (upper) on Cruise 7205.

Saury eggs were taken in 18 oblique net hauls of which 16 were from the regular CalCOFI grid and two from offshore (Figure 4). No collections contained more than seven eggs and 11 collections contained but a single egg, hence large clusters of eggs were lacking. Of the seven collections with two or more eggs, four contained eggs with two stages of development, representing two days' spawning.

Saury eggs appear to be equally well (or poorly) collected by both types of gear; approximately 10% of the neuston hauls contained saury eggs, compared to circa 12% for oblique hauls.

Saury larvae-juveniles present quite a different picture. Larvae-juveniles of saury were taken in 74 of the 148 stations occupied with neuston gear on Cruise 7205, i.e., in 50% of the stations occupied; whereas these stages were obtained in only six oblique hauls, i.e., in 4% of the stations occupied. This is a dramatic difference.

Sampling with the neuston gear is even better than one would conclude from the above figure of 50% positive hauls. In the northern part of the survey pattern it was too early in the year for full saury spawning—rather spawning was just commencing in the waters off Washington and Oregon. Likewise, in the southern part of the pattern, particularly inshore off southern Baja California, we did not get saury spawning because this was beyond the southern limit of saury spawning. In the intermediate area—off northern Baja California and southern California, sauries were sampled at most stations occupied.

In addition to Pacific saury, *Cololabis saira*, there is a small tropical saury, *C. adocetus* Bohlke, in the eastern North Pacific. The dwarf species was taken at all stations occupied between 20.125 to 20.145 inclusive on the southernmost offshore line along 20° N latitude. The best method of distinguishing between these two species is by number of vertebrae. Specimens of *C. adocetus* had 56 to 58 vertebrae in contrast to those of *C. saira* which had 63 to 68. The young stages of the two species are remarkably similar in appearance otherwise. The caudal peduncle character given by Ueyanagi and Doi (1971) for distinguishing between specimens of the two species could not be consistently applied to our specimens. The positioning of the last finlet of the dorsal and anal fins in relation to the caudal fin was too similar on some specimens of both species to be a reliable character. Hence we relied on vertebrae counts made from radiographs for positive identifications.

Obviously the neuston net is a highly effective gear for sampling larvae-juveniles of saury, which live exclusively near the surface. The distributional pattern we obtained from neuston hauls on extended

Cruise 7205, including the sharp separation of the two species of *Cololabis,* was much better than the composite pattern based on positive hauls for saury larvae-juveniles from all previous offshore CalCOFI cruises.

Jack Mackerel (Eggs and Larvae), *Trachurus symmetricus* (Ayres)

The offshore distribution of eggs and larvae of the jack mackerel, *Trachurus symmetricus,* was seldom completely circumscribed on our regular CalCOFI cruises (Ahlstrom, 1969). One of the objectives of extended Cruise 7205 was to obtain information on the offshore distribution of eggs and larvae of this species. Farris (1961) showed that May was usually the peak month for eggs and June for larvae of *Trachurus symmetricus.*

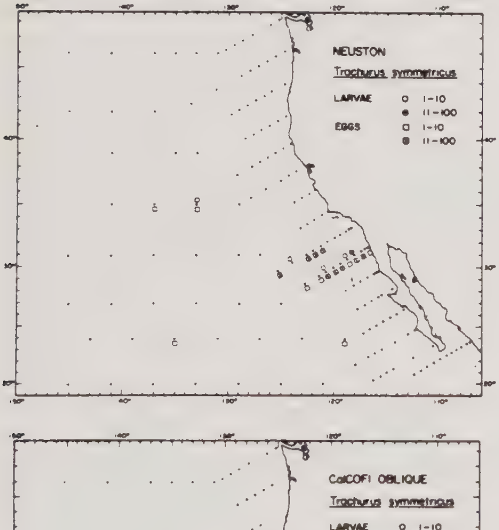
NEUSTON
Trachurus symmetricus
LARVAE
○ 1-10
● 11-100
EGGS
□ 1-10
■ 11-100
CalCOFI OBLIQUE
Trachurus symmetricus
LARVAE
○ 1-10
● 11-100
EGGS
□ 1-10
■ 11-100
■ 101-1000
150°
140°
130°
120°
110°
40°
30°
20°

FIGURE 5. Distribution and relative abundance of eggs and larvae of jack mackerel, *Trachurus symmetricus,* taken in neuston hauls (upper) and CalCOFI oblique hauls (lower).

Although jack mackerel eggs and larvae were taken in both types of plankton hauls (Figure 5), the eggs and larvae occurred in more oblique hauls than in neuston net hauls. This was particularly true of the larvae; jack mackerel larvae were taken in only six neuston net hauls as compared to 25 oblique hauls. Moreover, only small jack mackerel larvae, 1.7 to 3.5 mm, were taken in the neuston collections; whereas, larvae up to 15.0 mm were taken in the oblique hauls. Hence, larger larvae of jack mackerel do not congregate near the surface as do those of the northern anchovy. Jack mackerel eggs, however, are collected relatively well in surface neuston hauls—occurring in 16 hauls as compared to 23 oblique hauls. Jack mackerel eggs previously had been found in some abundance near the surface (Ahlstrom, 1959; Bieri, 1961), hence their presence in the neuston net hauls was not unexpected.

Sablefish (Larvae), *Anoplopoma fimbria* (Pallas)

Larvae of the sablefish were taken in seven collections with most specimens taken at station 20.20 (Figure 6). A size series of 443 specimens, 9.0 to 33.0 mm, was obtained at this station. No specimens of sablefish larvae were taken in oblique plankton hauls on Cruise 7205. The large collection of sablefish from station 20.20 contained more specimens than the aggregate of all specimens collected previously in oblique hauls on CalCOFI cruises. A complete size series was available from this one haul—which we have used for illustrations (Figure 7). The larvae are slender, heavily pigmented and develop strikingly large, but distinctively pigmented pectoral fins. Brock (1940) called attention to the large pigmented pectoral fins, one-third the standard length, that

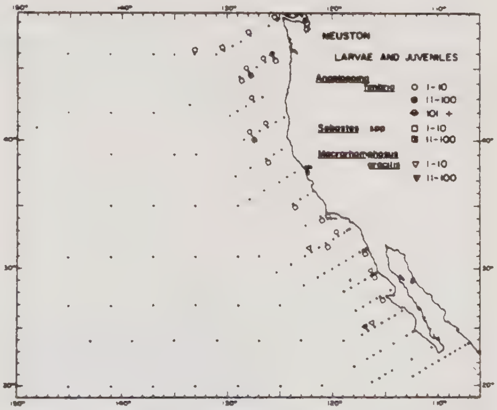
NEUSTON
LARVAE AND JUVENILES
Anoplopoma fimbria
○ 1-10
● 11-100
● 101 +
Sebastes spp
□ 1-10
■ 11-100
Macrorhamphosus gracilis
▽ 1-10
▼ 11-100
150°
140°
130°
120°
110°
40°
30°
20°

FIGURE 6. Distribution and relative abundance of larvae and early juveniles of the sablefish, *Anoplopoma fimbria;* rockfishes, *Sebastes* spp.; and slender snipefish, *Macrorhamphosus gracilis,* in neuston collections on Cruise 7205.

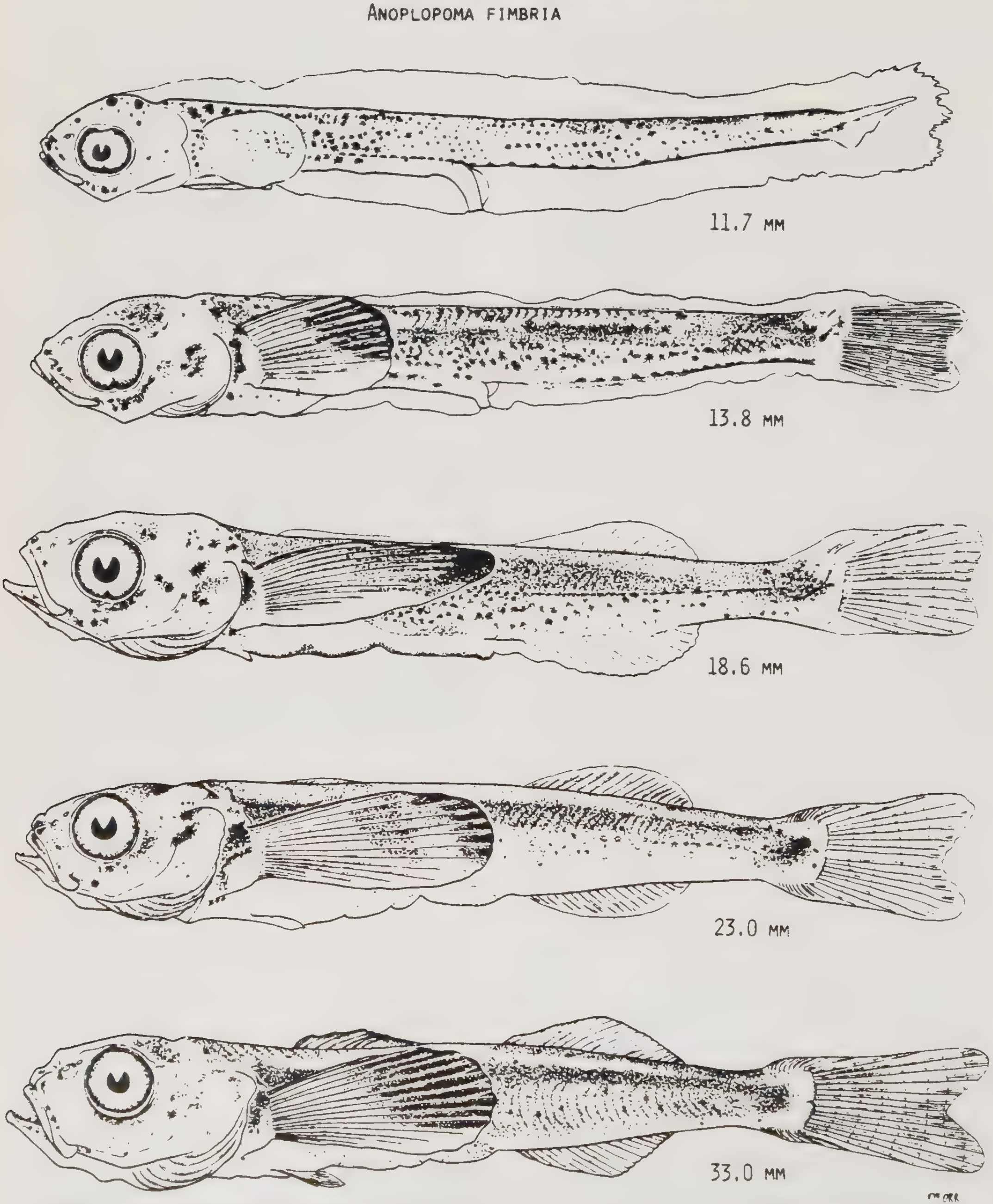
ANOPLOPOMA FIMBRIA
11.7 MM
13.8 MM
18.6 MM
23.0 MM
33.0 MM

FIGURE 7. Larval developmental series of sablefish, *Anoplopoma fimbria,* based on neuston collections made at CalCOFI station 7205-20.20. Measurement given under figures are standard length.

develop on late-stage larvae of sablefish. Kobayashi (1957) described a larval series, with illustrations of five specimens, 11.3 to 30.2 mm total length. Our specimens are similarly shaped, but more heavily pigmented on the back and particularly more heavily pigmented on the outer margins of the pectoral fins.

Rockfish (Larvae), *Sebastes* spp.

Rockfish larvae were taken in 16 neuston collections (Figure 5). the two largest collections were obtained at stations 20.50 (60 specimens 8.5 to 15.0 mm) and 40.80 (48 specimens 14.5 to 31.0 mm). The latter collection, especially, contained larger sized specimens, seldom obtained in oblique plankton hauls. Rockfish larvae were taken in 38 oblique plankton hauls; the number of specimens per collection ranged from one to 55. The difference in size composition of the specimens taken by the two types of gear is quite dramatic. Of the 138 specimens taken in neuston collections, only 16 were 10.0 mm or less in standard length, 78 were in the size range of 10.1 to 20.0 mm, and 44 were 20.1 to 33.5 mm. In contrast, 298 of the 308 specimens taken in oblique hauls were 10.0 mm or less in body length and only 10 specimens were larger than 10.0 mm, i.e., 10.1 to 17.0 mm. Obviously larger size specimens of rockfish still in the pelagic stage do tend to congregate at the surface. Most rockfish in the neuston hauls appear to be a single species; although specimens could not be identified with certainty, *Sebastes alatus* is a possibility.

Slender Snipefish (Larvae-Juveniles), *Macrorhamphosus gracilis* (Lowe)

Larvae of this species are occasionally taken in CalCOFI collections. Specimens were obtained in four neuston collections (Figure 5); with most specimens in the collection taken at station 130.80, where 38 specimens ranging in length from 8.0 to 17.5 mm were caught. This is another instance in which the neuston collections contained both more specimens and larger sizes than were taken in oblique hauls. As Fitch and Lavenberg (1968) recorded, this species is a schooling fish usually occurring in small schools of 50 to 100 individuals, but on one occasion off southern California, fishermen set on a school estimated to contain 40 to 50 tons. No material of this species was obtained in the oblique plankton hauls made on extended Cruise 7205.

Family Myctophidae

The early developmental stages of myctophids are sharply separable into two groups, those that have narrow-eyed larvae and those that have round-eyed larvae. The myctophids in the first group belong to the subfamily Myctophinae, those in the second group to the subfamily Lampanyctinae (Paxton, 1972; Moser and Ahlstrom, 1972, 1974).

The family Myctophidae was well represented in neuston net collections, inasmuch as larvae and/or juvenile-adults were obtained for 15 genera—eight in the subfamily Myctophinae, seven in the subfamily Lampanyctinae. Equal numbers of specimens were obtained of each subfamily in neuston hauls, 407 as compared to 407. What was completely unanticipated was that all specimens except one of Myctophinae taken in neuston hauls were juvenile-adults, whereas all specimens of Lampanyctinae were exclusively larvae.

Subfamily Myctophinae

As noted above, all specimens of this subfamily taken in surface neuston collections, save for one larva, were juvenile-adults, including recently transformed specimens, belonging to eight genera. In contrast, the collections of this subfamily from oblique plankton hauls contained only larvae, save for one juvenile of *Diogenichthys atlanticus*. Larval material was obtained of the eight genera sampled in neuston hauls, and of two additional genera (*Protomyctophum* and *Electrona*). Hence, for members of this subfamily the two types of gear sampled different developmental stages.

Most material of this subfamily in neuston collections was obtained over the regular CalCOFI grid—393 of 407 specimens. In contrast, larvae of this subfamily were slightly more abundant in the offshore grid of stations in oblique plankton hauls, the average number per collection was 14 in the offshore grid, 12 over the regular CalCOFI grid.

The several kinds of juvenile-adult myctophids of the subfamily Myctophinae taken in neuston net hauls belong to species that commonly have been dipnetted under working lights of our research vessels while on station.

The four genera of myctophids known collectively as the slendertails are among the lanternfishes that are known to occur at the surface. The most common species of slendertails in the neuston net hauls was *Tarletonbeania crenularis* (Figure 8, upper); 296 specimens, 20.5 to 67.0 mm standard length were obtained from 12 hauls, preponderantly from the northern part of the regular CalCOFI pattern, i.e. lines 10 to 30 off Washington and Oregon. Its southern counterpart, *Gonichthys tenuiculus*, was taken in 13 collections from the southern part of the CalCOFI pattern, but in lesser abundance (Figure 8, upper), 46 specimens total, 14.5 to 57.5 mm standard length. Only single specimens of early juveniles were obtained of the other two genera of slendertails, a 24.0 mm specimen of *Loweina rara*, and a 16.5 mm specimen of *Centrobranchus choerocephalus*.

Among other Myctophinae lanternfishes only juveniles of *Hygophum atratum* were taken in any abundance in neuston hauls—56 specimens, 13.5 to 47.5 mm standard length from six stations off central and southern Baja California.

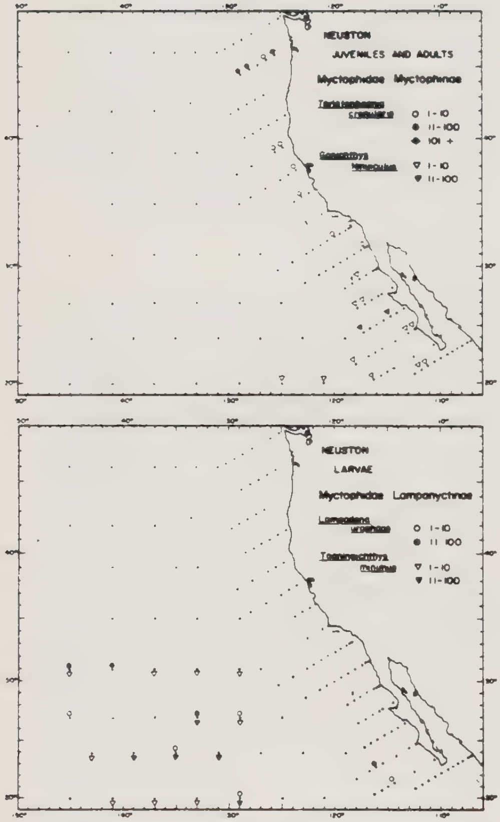

FIGURE 8. Upper—Distribution and relative abundance of juveniles and adults to two slendertails, *Tarletonbeania crenularis* and *Gonichthys tenuiculus* (Family Myctophidae, Subfamily Myctophinae). Lower—Distribution and relative abundance of larvae of two lanternfishes *Lampadena urophaos* and *Taaningichthys minimus* (Family Myctophidae, Subfamily Lampanyctinae).

Subfamily Lampanyctinae

Only larvae of lanternfishes of this subfamily, not juvenile-adults, were taken in neuston net hauls. The material from oblique plankton hauls consisted predominantly of larvae, together with a few juvenile-adult specimens. There is little relation between the kinds and relative abundance of myctophid larvae sampled by the two kinds of gear.

Only three kinds of lampanyctine larvae were taken at all commonly in neuston net hauls: *Taaningichthys minimus, Lampadena urophaos,* and *Bolinichtys* sp. In addition, four kinds were taken infrequently: *Ceratoscopelus* sp., *Diaphus* sp., *Lampanyctus* sp., and *Stenobrachius leucopsarus.*

Larvae of *T. minimus* furnish a prime example of a species taken in markedly greater abundance in neuston collections. Larvae of this species, ranging from 4.0 to 20.0 mm long, were obtained at 14 neuston stations, averaging 10 larvae per positive haul (Figure 8, lower). In oblique plankton hauls a total of three specimens, 3.0 to 9.0 mm long, was obtained in as many hauls. It should be noted that the size range sampled in neuston hauls is from early stage larvae to larvae about ready to metamorphose, i.e., all sizes of larvae of this species occur in the surface layer sampled by the neuston net. Adults of this species occur predominantly at depths between 450 and 500 m, and do not appear to perform daily vertical migration (Davy, 1972). Even so, the adults probably do migrate to the upper mixed layer to spawn; otherwise there is no obvious mechanism for the larvae to get to the surface layer from the depths at which the adults live.

Larvae of *L. urophaos* and *Bolinichthys* sp. were taken in larger numbers per collection in neuston hauls, but occurred in more than twice as many oblique hauls as neuston. A total of 162 specimens of *L. urophaos* larvae was taken in nine neuston collections, an average of 18 specimens per positive haul (Figure 8, lower). Larvae of this species were taken in 20 oblique hauls, but in lesser abundance—averaging only four specimens per positive haul.

Larvae of *Bolinichthys* sp. were taken in 13 oblique hauls as compared to six neuston hauls; however, the latter yielded 38 larvae as compared to a total count of 28 for oblique hauls.

For all other categories of lampanyctine lanternfishes, the oblique hauls obtained decidely more larvae in more collections. Several examples follow.

Larvae of *Ceratoscopelus* sp. were taken in five neuston hauls for a total count of 38, whereas larvae of *Ceratoscopelus* sp. occurred in 40 oblique hauls for a total count of 657.

Larvae of *Stenobrachius leucopsarus* were taken in five neuston hauls (total of six specimens) as compared to 48 oblique hauls in which 372 specimens were obtained. For the other two kinds of lampanyctine larvae taken in neuston hauls, *Diaphus* had three occurrences for a total of five specimens, and *Lampanyctus* had six occurrences for a total of eight as compared to 31 occurrences and 133 specimens of *Diaphus* and 96 occurrences and 460 specimens of *Lampanyctus* in oblique hauls.

Although larvae of *Triphoturus mexicanus* and *T. nigrescens* were not taken in neuston hauls, they occurred in 46 oblique hauls, contributing 460 specimens.

DISCUSSION

Most kinds of fishes taken commonly in the CalCOFI neuston collections or species closely related to these have been taken in other areas in neuston hauls (Hempel and Weikert, 1972; Nellen, 1973). For example, there is a striking similarity between the forms taken in neuston hauls in the vicinity of the Meteor Seamount in the eastern Atlantic (Nellen, 1973). The four most common kinds were *Scomberesox saurus*, the Atlantic equivalent of the Pacific saury, 57.3% of total; *Macrorhamphosus* sp., 36.2%; *Gonichthys cocco*, 3%; *Taaningichthys* sp., 0.6% for a composite total of 97.1%.

Advantages and Disadvantages of Neuston Net Collections

We propose to give a brief summary of the advantages and disadvantages of neuston net collections. For fishes that congregate near the surface at any stage in their early development—from eggs, larvae, to juvenile stages the neuston net is a good gear for establishing areal distribution and even relative abundance. For example, the distribution of the Pacific saury, based on neuston net hauls on Cruise 7205, provided a more coherent distributional pattern than was obtained from composite oblique plankton hauls records from a number of previous CalCOFI cruises. Furthermore, the distribution of the small tropical saury, *Cololabis adocetus,* could be sharply delimited from that of the Pacific saury, *C. saira.* The sablefish, *Anoplopoma fimbria,* was markedly more abundant in neuston net hauls and a larger size range of specimens was sampled than have been taken in oblique hauls. The lanternfish, *Taaningichthys minimus,* appears to prefer the surface layer at all stages of larval development.

For some kinds of fishes, larger sized specimens are taken in neuston hauls than in oblique hauls. A number of examples were given in the preceding discussions. For example, strikingly more larger anchovy larvae were taken in neuston hauls than in oblique; the size composition of rockfishes, *Sebastes* spp. taken by the two types of hauls also was markedly different, with larger sized specimens predominating in the neuston hauls. However, larvae of jack mackerel, *Trachurus symmetricus* proved an exception in that only small larvae were taken in neuston hauls, compared to a larger size range of larvae in oblique hauls. For some fishes, a different developmental stage was sampled by the neuston haul; thus, only juvenile-adult material of myctophine lanternfishes was taken in neuston hauls, whereas the complete size range of larvae of these lanternfishes was obtained in oblique hauls.

The marked difference in size composition of anchovy larvae in the neuston hauls as compared to standard oblique hauls points up the fact that the neuston hauls collect a disproportionate number of larger larvae while markedly undersampling the smaller sizes. What are the implications of these differences with regard to mortality estimates? A first reaction is that the neuston sample is a highly biased one, of dubious value for mortality studies. But the neuston haul does provide a much larger sample of anchovy larvae in the size range of 14 mm and larger—sizes that are poorly sampled in oblique hauls. On reconsideration, why not take advantage of this fact. If additional work with neuston hauls shows that the larger sized larvae of anchovies are consistently sampled by the neuston net from station to station and cruise to cruise, then this net could be used to provide estimates of changes in relative abundance of larger anchovy larvae from year to year—information essential for evaluating success of survival of cohorts of anchovies.

Although some species are sampled more abundantly in neuston hauls, the reverse is also true. Many kinds of larvae common in oblique hauls are rare or lacking in neuston collections. This net alone will not provide a representative sample of the fish larvae in a survey area. It should not be regarded as a primary tool, but a supplementary one with intriguing potentials.

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Memorias del Simposio sobre Biología y Dinámica
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DISTRIBUCION BATIMETRICA DE *PLEURONCODES PLANIPES* STIMPSON (CRUSTACEO; GALATEIDO)

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RESUMEN

Estos crustáceos constituyen en aguas de California un recurso marino de importante potencial pesquero y en la actualidad está empezando a considerarse su explotación para tratar de desarrollar su pesca con la mayor eficacia. Por lo tanto es interesante obtener detallada información sobre la distribución de estos animales en la región de California. Se presentan aquí los datos correspondientes a la distribución de Pleuroncodes planipes (langostillas) en la región de California durante las cuatro estaciones de 1969, para lo cual se han estudiado las muestras de plancton obtenidas con redes BONGO de apertura y cierre automático. Las muestras de plancton fueron colectadas día y noche en cada localidad, a ocho niveles de profundidad, desde 600 m hasta cero metros.

P. planipes no apareció durante ninguna de las estaciones de 1969 en localidades frente a Monterrey y San Diego, California (Estados Unidos); pero se presentó muy abundante todo el año en las localidades investigadas frente a Punta Eugenia, Baja California (México). La mayor concentración de langostillas ocurrió en Septiembre y Diciembre en la zona del epiplancton de dicha región, siendo menos abundantes en Junio. Se observaron diferencias cuantitativas en las colecciones obtenidas de día y de noche en las mismas localidades y profundidades, registrándose concentraciones elevadas en los lechos más superficiales y viceversa, lo que indica que otros factores, además de la hora de captura, influyeron en las características que presenta la distribución batimétrica de estos animales. Se compara la distribución de las langostillas y otros zooplanctontes correspondientes a las mismas colecciones.

INTRODUCCION

Pleuroncodes planipes llamado comunmente langostilla aparece en grandes concentraciones en las regiones pelágica y béntica de California y Baja California (Boyd y Johnson, 1963) extendiéndose desde la costa hasta varias millas mar afuera. -- Longhurst (1969). Arvizu, García y Morales (1974) consideran que las langostillas constituyen un potencial de riqueza pesquera y en la actualidad se está iniciando la pesca de estos crustáceos (Kato, 1974). En toda pesquería es importante tener información sobre la distribución vertical y horizontal de la especie que se explota y los cambios que presenta en esos parámetros en relación con la estación del año y las horas del día y de la noche. En este trabajo se presenta la dis tribución batimétrica de las langostillas en las cuatro estaciones del año 1969, que constituyen los datos obtenidos al estudiar las colecciones de plancton correspondientes.

Las langostillas se alimentan de fitoplancton (Blackburn, 1968; Longhurst, 1967), aunque se considera que se trata principalmente de organismos omnívoros (Blackburn, 1968; Kato, 1974, Longhurst, Lorenzen, Thomas, 1967) pero estos crustáceos constituyen una parte importante en la dieta básica de varios peces - entre los que se encuentran los atunes (Alverson, 1963; Blackburn, 1968, 1969; Glynn, 1961; McHugh, 1962), otros peces (Arvizu, García y Morales, 1974), peces espada, aves marinas, focas (Boyd, 1969; Glynn, 1961; Kato, 1974) y ballenas (Matthews,1932). Scott y Flittner (1972) indican que las diferencias observadas en la distribución y comportamiento de los cardúmenes de atún-- (Thunnus thynnus) frente a Baja California estaban relacionadas con la presencia de P. planipes en aquellas zonas.

Estos galateidos pelágicos aparecen concentrados cerca de las regiones de surgencias (Blackburn, 1969) que son zonas ricas en fitoplancton. Así estos crustáceos se distribuyen -- frente a California (Boyd, 1967; Blackburn, 1968, 1969; Kato 1974; Longhurst, 1967, 1968; Longhurst y Seibert, 1971) y en - el Golfo de California (Arvizu, García y Morales, 1974; y datos personales). Brinton (en prensa) observa que durante el período Mayo-Junio de 1974 aparecían concentraciones de zoeas, postlarvas y algunos individuos adultos en localidades al Sur de Punta Eugenia, frente a Bahía Magdalena y frente al Cabo San - Lucas, Baja California y describe con detalle su distribución.

La distribución de las langostillas en la región Californiana aparece afectada por la Corriente de California y la Corriente de Davidson. Cuando esta última, que está constituída por aguas cálidas, es fuerte, favorece el transporte hacia el Norte de las poblaciones que habitan las aguas de temperatura elevada en aquella zona meridional y en consecuencia las poblaciones de langostillas, que normalmente habitan las regiones frente a Baja California, progresan hacia el Norte. -- Densas poblaciones de P. planipes avanzaron hacia el Norte durante los años 1958 al 1960 y de 1972 a 1973 (Kato, 1974) invadiendo las aguas de la parte Sur de California y eran lanzadas por el viento y el oleaje hacia las playas y costas de esta zona. Glynn (1961) hace referencia a progresiones similares de poblaciones de langostillas procedentes de las regiones cálidas del Sur avanzando por la región costera de California.

Estas grandes acumulaciones de langostilla resultan de interés particular para mí, ya que he observado situaciones similares frente a las costas del Noroeste de España. En aquella región el cangrejo pelágico *Polybius henslowi* Leach (Decápodo, Braquiuro) aparece abundante cuando aguas excepcionalmente cálidas bañan aquella región. *P. henslowi*, comunmente llamado patexto y patela, respectivamente en Galicia y Santander, aparece abundante de Abril hasta Agosto en las aguas Ibéricas, desde Cabo San Vicente hasta Tarifa, aunque no es frecuente en el Mediterráneo. Patexo es de importancia primordial en la dieta de los Túnidos del Atlántico Ibérico (De Buen, 1925; Held, 1938 y datos personales inéditos), de forma semejante al caso de *P. planipes* en aguas del Pacífico Noroeste. *P. henslowi* aparece en grandes concentraciones de individuos adultos y jóvenes en aguas de temperatura elevada y con este fenómeno coincide que las capturas de albacora (*Thunnus alalunga*) resultan ser más altas que las normales frente a las costas del Norte y Noroeste de España (datos inéditos personales). En aquella región, *P. henslowi* es arrastrado hacia las playas y bahías como sucede con *P. planipes* en las costas de California, aunque en cantidades mucho mayores en el Atlántico, llegando a varios millares de toneladas y esos cangrejos son entonces utilizados como fertilizantes por los granjeros, lo que contribuye a las excepcionales cosechas que se obtienen en aquella región española.

MATERIAL Y METODOS

Las colecciones de plancton que se analizaron corresponden a los cruceros realizados por la Cooperativa de Investigacionesde Pesca Oceánica de California (CalCOFI) en las cuatro estaciones de 1969. Así los cruceros de invierno corresponden a los meses de Febrero-Marzo (6902-03), los cruceros de Primavera, Mayo-Junio (6905-06), los del Verano se efectuaron en los meses de Agosto-Septiembre (6908-09) y los cruceros de Otoño corresponden a Noviembre-Diciembre (6911-12). El plancton se colectó con redes BONGO de apertura y cierre automáticos (McGowan y Brown, 1966).

Las posiciones en la línea 120 (la más meridional ocupada) corresponde a los meses de Marzo, Junio, Septiembre y Diciembre de 1969, para los cruceros CalCOFI arriba mencionados. De ahí que, al analizar la distribución de *P. planipes* en las varias estaciones del año, se indica usualmente el mes a que pertenecen los referidos datos.

El número de langostillas colectadas no se determinó en cada caso, solamente para las colecciones de los cruceros --

6909 y 6912, así como en tres casos, cuando se obtuvieron 21 colectas positivas para este crustáceo durante los cruceros 6903 y 6905. Pleuroncodes planipes no constituía el objetivo principal de mis estudios al examinar dichas muestras de plancton, de ahí que no considerase entonces de interés la distribución cuantitativa de estos crustáceos. Sin embargo, con los datos numéricos que ha determinado puedo estimar que las concentraciones de P. planipes son mayores en número de individuos y en espacio ocupado por sus poblaciones en los meses de Septiembre y Diciembre que en Febrero y Junio.

Estas colecciones de plancton corresponden a una serie de localidades ocupadas a lo largo de las líneas 7o. 9o. y 12o. en la zona de CalCOFI en la región de California y Baja California. Las pescas de plancton se efectuaron de día y de noche en la misma localidad y a las mis-- mas profundidades. Las pescas de día se obtuvieron antes del mediodía o a primeras horas de la tarde y las pescas de noche se tomaron antes de media noche, justamente a media noche o inmediatamente después. De esta forma las pescas de día y de noche en la misma localidad corresponden a un período de doce horas aproximadamente.

En la Primavera, Verano y Otoño se obtuvieron las colecciones de plancton a profundidades de 600-475, 475-350, 350-225, 225-100, 100-75, 75-50, 50-25, 25-0 metros y en el crucero de Inviero desde aproximadamente 350-225 o de 300-250, 250-200, 200-150, 150-125, 125-100, 100-75, 75-50, 50-25, 25-15, 15-0 metros.

En teoría, el número de ejemplares colectados en las redes BONGO de la derecha e izquierda, denominadas también estribor y babor, corresponde a 1,000 m^3 de agua filtrada. La velocidad del arrastre en los intervalos de 25 m en el estrato de 100 m de la zona eufótica será más lenta que en los estratos por debajo de los 100 m, donde el muestreo ocupa bandas de 125 m de profundidad, para en ambos casos obtener 1,000 m^3 de agua filtrada. De ahí que, aunque la cantidad de agua filtrada es aproximadamente la misma en los estratos de 25 m y de 125 m de altura, la velocidad del arrastre en los estratos más superficiales ha de ser 5 veces más lenta que en los estratos de 125 m de altura. Se precisa establecer un método para calibrar y poder comparar cuantitativamente los datos obtenidos en los estratos superficiales y profundos (Kramer y Ahlstrom, 1968).

Así el número de individuos se normaliza para los 1,000 m^3 para cada 25 m de profundidad por la fórmula:

$$N = N \frac{(\text{profundidad de apertura} - \text{profundidad de cierre})}{25}$$

N = número de individuos calculados
n = número de ejemplares para las redes de babor y estribor del par BONGO

DISTRIBUCION BATIMETRICA

Pleuroncodes planipes no se observó en ninguna de las estaciones del año 1969 frente a Monterrey o frente a San Diego, respectivamente en las líneas de posiciones 70 y 90; pero sin embargo era abundante en todas las épocas del año en las localidades ocupadas frente a Punta Eugenia, Baja California, México (línea 120), una región donde esta especie aparece constantemente durante todo el año.

La ausencia de langostillas en aguas del Sur de California en 1969 es normal si se consideran las condiciones oceánicas que prevalecieron durante ese año en aquella región. Los análisis del zooplancton correspondientes a las mismas colecciones de plancton, en lo que respecta a los Quetognatos, Sifonóforos, Medusas y Ctenóforos, indican que el año 1969 se caracteriza por una Corriente de California ni fuerte ni débil y que en la región de California prevalecieron temperaturas normales durante todo ese año (Alvariño, 1964, 1965, 1966, 1974 y datos inéditos). Las langostillas se presentan en aguas de la California meridional cuando la Corriente de California es extremadamente débil, permitiendo así la progresión intensa hacia el Norte de las poblaciones de *P. planipes* procedentes de sus dominios en aguas de Baja California. Por ejemplo en 1972 y 1973, un período de temperaturas cálidas poco usuales en California, cantidades enormes de *P. planipes* alcanzaron las aguas de la California meridional y así invadieron las riberas y las playas de esa región.

Los perfiles que se incluyen con la distribución de *P. planipes* en las cuatro estaciones del año, indican las capturas efectuadas respectivamente durante el día y la noche. Los segmentos verticales en dichos perfiles señalan las pescas efectuadas en donde no se presentaba este crustáceo (Figuras 1, 2, 3, 4).

P. planipes aparecía más abundante en las capas más superficiales del oceáno y ocupando una extensión más amplia en esa zona durante algunos períodos, como se puede observar por el número de ejemplares y el espacio ocupado por las poblaciones de este Galateido en la Tabla 1 y Figuras 1, 2, 3, 4.

Las poblaciones de P. planipes aparecen ocupando un espacio mayor en los lechos más superficiales durante el día, frente a Punta Eugenia, Baja California, en los meses de Septiembre y Diciembre y en las pescas nocturanas efectuadas también en Diciembre. Sin embargo, la abundancia númerica de las langostillas en ambos cruceros, para el Verano y el Otoño, resultaba más elevada de noche que durante las pescas de día. P. planipes se presentó en menor abundancia en Junio de 1969, tanto en las pescas de día como en las nocturnas. En Marzo, Junio y Diciembre, el espacio ocupado por las poblaciones de P. planipes era más amplio de noche que de día y también la especie era más abundante de noche.

Las langostillas realizan la puesta en Invierno, de Diciembre a Marzo, con un centro de puesta en la zona de la Bahía Magdalena (Boyd, 1960) o de Febrero hasta Marzo (Longhurst, 1969) para esta misma región. Sin embargo, Boyd (1960) indica que en plancton colectado frente a Baja California desde Enero hasta Julio, aparecían todas las fases larvales de las langostillas y Brinton (en prensa) las ha determinado en esa misma zona de Mayo a Junio de 1974.

El crucero de Mayo-Junio (6905-06) de 1969 coincidía por lo tanto con el final de la época de puesta para este crustáceo. Sin embargo, el espacio ocupado por la población era bastante reducido (Figura 2) y el número de ejemplares colectados fué también bastante reducido en esta época si se compara con los datos obtenidos para las otras estaciones. Verano y Otoño (correspondientes a los meses de septiembre y Diciembre) Figuras 3 y 4. La población de P. planipes aparecía en las muestras de Febrero-Marzo un poco más abundante que los mínimos correspondientes a Mayo-Junio de 1969. Figuras 1 y 2.

Las langostillas en las colecciones de 1969 alcanzaban una talla de 17 a 32 mm para la longitud del caparazón torácico, siendo más abundantes los ejemplares un poco más pequeños y un poco mayores que 25 mm de longitud de caparazón. De ahí que la población capturada podría considerarse representativa de una combinación de individuos jóvenes, adultos jóvenes y adultos, aún cuando estos últimos eran escasos. Boyd (1960) indica que las langostillas adoptan una vida estrictamente bentónica cuando el caparazón alcanza una longitud de 32 mm. En el material aquí analizado se observaron pocos ejemplares correspondientes a esa categoría, pero sin embargo su presencia se acusaba en las colecciones mesopelágicas , es decir, por debajo de los 475 m de profundidad. Esto indica que las poblaciones de *P. planipes* presentaba una estratificación ontogénica, así los individuos de mayor tamaño habitan estratos más profundos y los jóvenes los lechos más superficiales, relacionándose respectivamente con las poblaciones bentónicas y pelágicas que habitan esas mismas zonas.

P. planipes aparecía en la posición 120.45 en Junio y Septiembre de 1969 de los 600 a los 475 m de profundidad de noche y de día en Diciembre. No puede considerarse que esta distribución sea debida a un fallo de las redes que no cerraron bien, ya que los datos que he obtenido para la misma localidad y estaciones del año para las especies de Quetognatos, Sifonóforos y Medusas, indican que las especies aparecen a las profundidades que les corresponden (Alvariño, 1974 y datos inéditos). Así que, la distribución que se ha observado para las langostillas está confirmada en estas regiones, por la distribución de otras especies del zooplancton.

La distribución vertical que presenta *P. planipes* frente a Baja California durante las cuatro estaciones del año 1969 no muestra una relación bien definida con la distribución de la salinidad, oxígeno y en general con la temperatura, aún cuando la posición de la termoclina podría considerarse de interés, como se explica a continuación.

Durante el crucero de Marzo de 1969, *P. planipes* aparece de día justamente por debajo de la termoclina, mientras que de noche, las langostillas se extendían tanto por encima, por debajo y en la región de la termoclina. *P.planipes* ocupaba en Marzo una región más extensa de noche que durante el día y las poblaciones aparecían también más próximas a la superficie durante la noche. Durante el día se tomaron muestras a varios estratos de profundidad y *P. planipes* aparecía únicamente en la estación 120.70 de los 125 a los 100 m de profundida. De noche, las langostillas se presentaban desde la localidad 120.70 hasta la costa como se indica a continuación:

En la localidad 120.70 desde los 125 a los 100 m de profundidad, en la localidad siguiente hacia la costa desde los 125 a los 0 m, pero estaba ausente de los 100 a los 50 m de profundidad y en la localidad más cercana a la costa (120.45) las langostillas ocupaban los estratos desde los 75 hasta los 25 m de profundidad. Figura 1.

En Junio de 1969, P. planipes aparecía solamente cerca de las costas de Punta Eugenia. Estas poblaciones se extendían de los 75 a los 50 m de profundidad durante el día, justamente por debajo de la termoclina; pero de noche las langostillas aparecían en la misma localidad, de los 75 a los 50 m y también de los 25 a los 0 m de profundidad, justamente por debajo y por encima de la termoclina. Además, en esta misma localidad cercana a la costa se observó una población de P. planipes que se extendía de los 600 a los 475 m de profundidad durante la noche. La presencia de las langostillas a esta profundidad podría estar relacionada con procesos de surgencias en esa misma región, un proceso indicado también por la distribución de las isohalinas y los zooplanctontes mesoplanctónicos que ha analizado también para estos mismos cruceros. Figura 2. Brinton sugiere (comunicación personal) que las langostillas podrían estar descendiendo en esos lugares a estratos más profundos buscando una localidad cercana a la costa para allí asentarse.

P. planipes aparecía en la región más oceánica investigada en Septiembre de 1969, desde los 225 a los 100 m de profundidad durante el día, en una zona por debajo de la termoclina. Las langostillas no se presentaron en la localidad -- 120.55, pero reaparecieron en la posición 120.45 próxima a la costa, a profundidades entre 225 hasta los 25 m. extendiéndose justamente hasta el nivel de la termoclina más superficial que aparecía los 25 m de profundidad apróximadamente. Estos organismos no se presentaban durante la noche en las localidades más oceánicas, pero se observaron a los 600 hasta los 475 m de profundidad y de los 75 a los 0 metros de profundidad en la localidad más costera. Figura 3.

En Diciembre de 1969 P. planipes aparecía durante el - día en la localidad más oceánica investigada y en las dos posiciones cercanas a la costa, pero no se observó en la región entre estas dos localidades extremas investigadas. La población más oceánica aparecía a los 75-25 m de profundidad, por encima de la termoclina. En las localidades más costeras, las langostillas se extendían así mismo de los 75 a los 25 m de profundidad y en la localidad más costera se encontró una población profunda de langostillas a los 600-475 m de profundidad, similar a la situación observada en Septiembre para la misma localidad, mientras que la población epipelágica - aparecía de los 225 a los 25 m de profundidad. En Diciembre de 1969 las langostillas aparecían en las pescas nocturnas en todas las localidades investigadas desde mar afuera hasta la zona nerítica. En las dos localidades más oceánicas aparecían entre los 225 a los 75 m y de los 225 a los 0 metros de profundidad respectivamente, estando ausentes en los estratos entre 100 a los 75 m de profundidad en la segunda localidad en dirección a la costa (120.70). En la posición más cercana a la costa (120.45) las langostillas se encontraron a 100-25 m de profundidad, mientras que en la próxima localidad hacia mar afuera (120.55) se observaron unicamente entre los 50 a los 25 m de profundidad (Figura 4). Durante el día las poblaciones de *P. planipes* se extendían por encima de la termoclina en las localidades más apartadas de la costa y por debajo o llegando hasta la zona de la termoclina en las localidades neríticas. Durante la noche, las langostillas aparecían por encima, por debajo y en la región de la termoclina.

En el Invierno, Crucero 6902-03, las poblaciones de langostillas representadas en las muestras de plancton, se encontraban en aguas oscilando entre 15.4 y 19°C y una población que se observó de noche en la posición 120.55 a 125-100m de profundidad ocupaba aguas con temperaturas entre 11.5 y 12.5°C.

En el crucero de Primavera (6905-06) *P. planipes* se presentaba en la zona del epiplancton en aguas con temperaturas entre 11 y 17°C y la población profunda, por debajo de los 475 m de profundidad se encontraba en aguas con una temperatura máxima que alcanzaba solamente los 7.5°C.

En el Verano (Crucero 6908-09) las poblaciones epiplanctónicas de langostillas aparecían en aguas con temperaturas entre 9 y 20.5°C aproximadamente y las poblaciones mesopelágicas la temperatura máxima que encontraban alcanzaba solamente a los 7°C. La mayor concentración numérica de *P. planipes* observada en esta época del año aparecía de noche en la posición 120.45 a una profundidad de 50-25 en aguas con temperaturas entre 16 y 20.4°C.

En el Otoño (Crucero 6911-12) *P. planipes* aparecía en la región epipelágica en aguas con temperaturas oscilando entre 10 y 19°C y en la zona mesopelárgica en aguas a menos de 7.5°C de temperatura. En esta época del año se observó una concentración numérica elevada de langostillas en la posición 120.45 durante la noche, a una profundidad entre 50-25m y en aguas con temperaturas entre 14.9 y 20.5°C.

No se observó una relación bien definida entre la distribución batimétrica de *P. planipes* y la distribución de la salinidad y la densidad de las aguas, aún cuando se nota una cierta relación con la temperatura según se ha señalado. El contorneado que presenta la distribución de la población profunda de P. planipes en Diciembre de 1969 coincidía aproximadamente con la isopleta de 2 ml de oxígeno por litro.

Se decidió establecer un análisis comparativo entre la distribución batimétrica de P. planipes y la distribución de las varias especies de Quetognatos, Sifonóforos y Medusas determinadas para la misma serie de colecciones de plancton (Alvariño, 1974 y datos inéditos). Así se observó que las poblaciones profundas de P. planipes debían proceder de la zona - bántica alcanzando así los niveles del mesoplancton al ser desplazadas por las surgencias que se producían en esas zonas. Así mismo se observó que la distribución de los Quetognatos bati- y mesopelágicos, Sagitta macrocephala, S. maxima, S. - zetesios, Eukrohnia fowleri (Alvariño, 1974 y datos inéditos) coincidía perfectamente con la distribución de las poblaciones profundas de P. planipes determinadas en estas colecciones y también con los fenómenos de surgencia.

Hay sin embargo que considerar que no se ha de esperar - una perfecta coincidencia en la distribución de P. planipes y las especies típicas del zooplancton y aún cuando a veces una cierta coincidencia es evidente entre la distribución de P. planipes y la distribución de varias especies de Quetognatos, podría ser simplemente accidental, o relacionada con la dinámica oceánica en aquellas localidades. Para comprender mejor estas relaciones se precisaría llevar a cabo un análisis más detenido y con mayor número de muestras de plancton. Hay que establecer que han de existir evidentemente diferencias ecológicas y de comportamiento al comparar la distribución de P. planipes (animales nectónicos) y la distribución de los Quetognatos planctónicos. Además, hay que considerar que la circulación oceánica en la zona de Punta Eugenia, incluyendo remolinos, surgencias y corrientes han de afectar con mayor intensidad a los animales del plancton que a los organismos del necton como P. planipes.

Las variaciones que se observaron en la distribución de P. planipes durante el día y la noche en las mismas localidades pueden ser ocasionadas por cambios en las condiciones ambientales, entre las que se cuentan, la concentración de alimento y depredadores, que de alguna forma han de afectar a la concentración o dispersión de las poblaciones de langostillas. La acumulación de alimento contribuiría a la concentración de estos animales (Blackburn, 1961) y la concentración de depredadores devorando langostillas activamente, contribuiría a su dispersión y escasez. Las variaciones numéricas entre las capturas diurnas y nocturnas podrían ser ocasionadas también, porque durante el día las langostillas pueden escapar más fácilmente que de noche.

Los datos obtenidos sobre la distribución batimétrica de *P. planipes* indican la presencia de dos poblaciones, una epipelágica habitando los estratos oceánicos por encima de los 200 m y una población mesopelágica, de la cual solamente la parte menos profunda, de los 600 a los 475 m aparecía representada en las muestras, extendiéndose por debajo de los 475 m de profundidad, podría considerarse que esta población mesopelágica es la cresta de una población que pululaba nadando por encima de las poblaciones asentadas en las inmediaciones del bentos. *P. planipes* no ha sido observado en los lechos entre 225 y los 475 m de profundidad, durante cualquiera de los cruceros efectuados en 1969 y este hecho podría considerarse como una evidencia de que no existen desplazamientos en masa de poblaciones de *P. planipes* entre los lechos profundos (475 m) y la zona eufótica oceánica y que ambas poblaciones son aparentemente independientes. Sin embargo, es posible que existan desplazamientos verticales de individuos entre las poblaciones epipelágicas y las mesopelágicas. El hecho de que tales migraciones no fuesen determinadas con el análisis de las colecciones de plancton, indica que los desplazamientos que se efectuan no son en masa, sino que se producen en grupos pequeños esparcidos, o individuos aislados. Las observaciones realizadas sobre la distribución de *P. planipes* indican que este crustáceo aparece representado en el plancton solamente en las regiones donde existe en densas concentraciones. Es de interés por lo tanto hacer resaltar que los individuos capturados en las pescas profundas correspondían a las poblaciones más costeras y en los lugares donde se producen frecuentemente fenómenos de surgencias de aguas profundas.

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TABLA I. DISTRIBUCION BATIMETRICA DE *Pleuroncodes planipes* Stimpson, EN AGUAS DE CALIFORNIA.

CRUCERO		D I A				N O C H E			
POSICION	LOCALIDAD	HORA FECHA	PROF. METROS	BONGO BAB.	BONGO EST.	HORA FECHA	PROF. METROS	BONGO BAB.	BONGO EST.
6902-6903									
26°53'N	120.70	1248	125-100	+		0318	125-100	+	+
117°10'W		7-III-69				7-III-69			
							100-75	+	+
							75-50	+	+
27°23'N	120.55					0112	125-100	m	m
116°12'W						6-III-69			
						2020	50-25	+	
						5-III-60	25-15	+	
						2126	15-0		+
						5-III-69			
27°43'N	120.45					0145	75-50		1
115°33'W						5-III-69			
							50-25	+	+
6905-6906									
27°54'N	120.45					2330	600-475		+
115°33'W						23-VI-69			
		0910	75-50	1	1	2100	75-50	+	+
		23-VI-69				23-VI-69			
							25-0	+	+
6908-6909									
26°17'N	120.90	0915	225-100	15					
118°24'W		29-IX-69							
26°53'N	120.70	0915	225-100	5	10				
117°10'W		28-IX-69							
27°43'N	120.45	0955	225-100		5	2120	600-475		15
115°33'W		26-IX-69				25-IX-69			
		1325	100-75		2	0004	75-0	17	
		26-IX-69				26-IX-69			
			75-50	5	2		50-25	51	61
			50-25		2		25-0	14	21
6911-6912									
26°17'N	120.90					2325	225-100	10	15
						9-XII-69			
							100-75		1
		0940	75-50		2				
		10-XII-69							
			50-25	1					
26°53'N	120.70					2325			
117°10'W						8-9-XII-69	225-100	40	15
						2140	75-50		1
						8-XII-69			
							50-0	1	2
							25-0		1
27°23'N	120.55								
116°12'W									
		0935	75-50		15	2145			
		7-XII-69				7-XII-69			
			50-25		6		50-25	14	27
27°43'N	120.45	1230	600-475		23				
115°33'W		6-XII-69							
			225-100	20	15				
		0930	100-0	4	20	2130	100-75	10	
		6-XII-69				5-XII-69			
			75-50	4	5		75-50	45	6
			50-25		23		50-25	99	107

La hora es local.

+ Langostillas aparecían en las muestras de plancton, pero no se obtuvieron datos numéricos.

m = muchas langostillas.

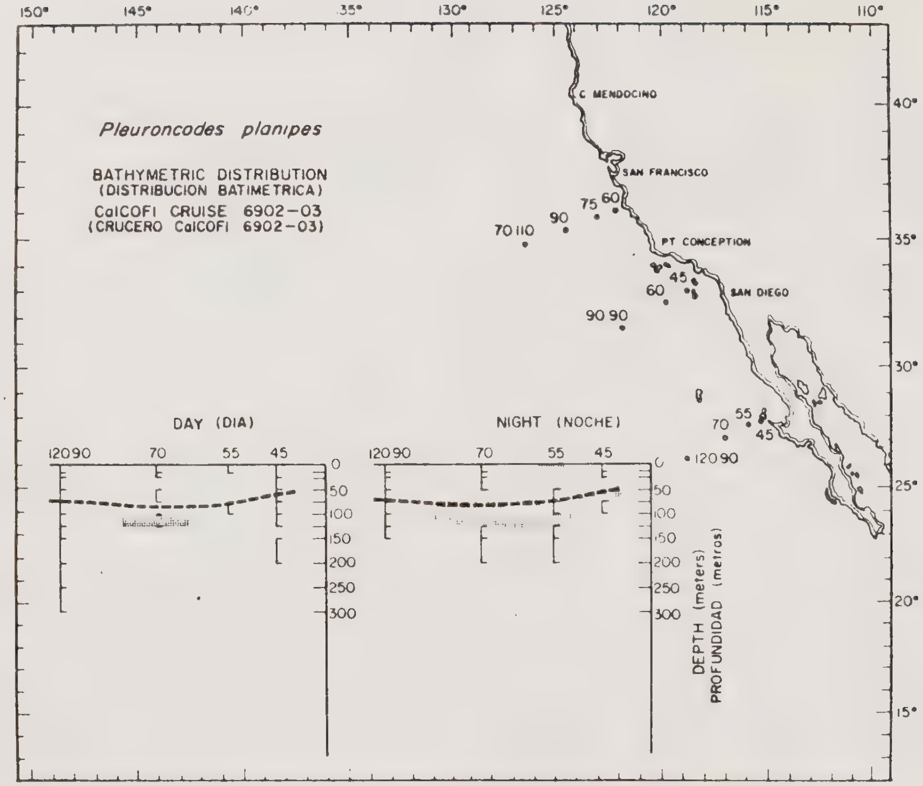
Pleuroncodes planipes
BATHYMETRIC DISTRIBUTION
(DISTRIBUCION BATIMETRICA)
CalCOFI CRUISE 6902–03
(CRUCERO CalCOFI 6902–03)
150°
145°
140°
135°
130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
15°
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
70 110
90
75
60
45
60
90 90
70
55
45
120 90
DAY (DIA)
NIGHT (NOCHE)
0
50
100
150
200
250
300
DEPTH (meters)
PROFUNDIDAD (metros)

Figura 1

Distribución batimétrica diurna y nocturna de Pleuroncodes planipes en aguas de California, durante el Invierno, Crucero Febrero-Marzo de 1969 (6902-03). Zonas sombreadas -- indican la distribución de este Galateido. Líneas verticales muestran las pescas en que la especie no aparecía. La línea de trazos gruesos señala la termoclina.

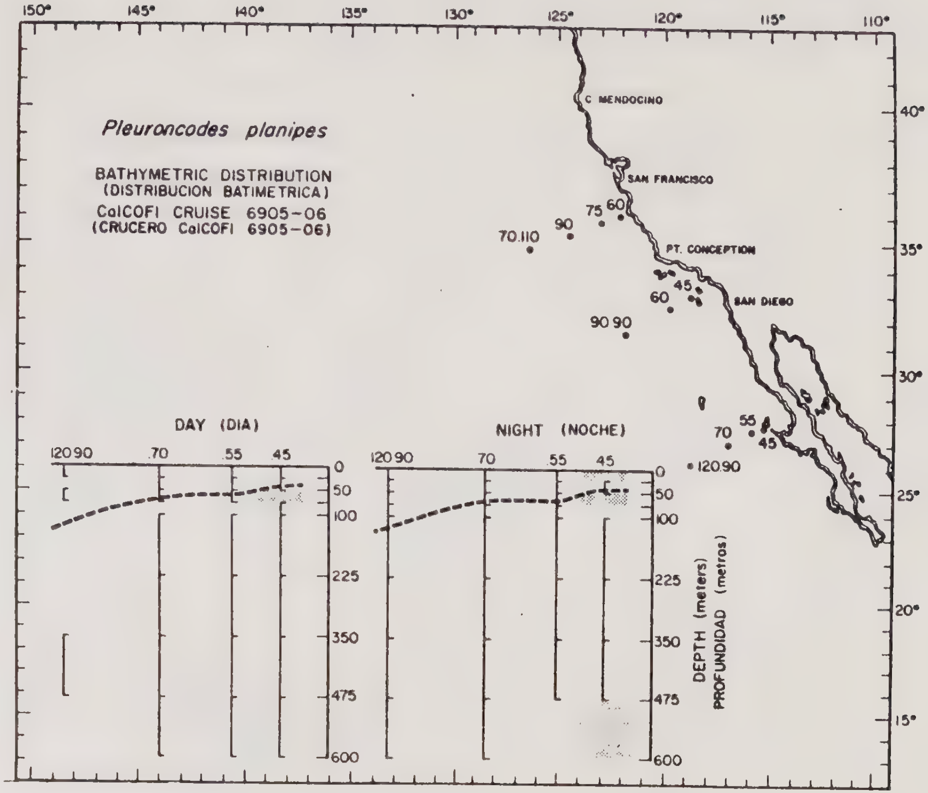
Pleuroncodes planipes
BATHYMETRIC DISTRIBUTION
(DISTRIBUCION BATIMETRICA)
CalCOFI CRUISE 6905-06
(CRUCERO CalCOFI 6905-06)
C MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
150°
145°
140°
135°
130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
15°
70.110
90
75
60
45
60
90 90
55
70
45
120.90
DAY (DIA)
NIGHT (NOCHE)
120.90
70
55
45
0
50
100
225
350
475
600
DEPTH (meters)
PROFUNDIDAD (metros)

Figura 2

Distribución batimétrica diurna y nocturna de Pleuroncodes planipes en aguas de California, durante la Primavera, --- Crucero Mayo-Junio de 1969 (6905-06). Zonas sombreadas -- indican la distribución de este Galateido. Líneas verticales muestran las pescas en que la especie no aparecía. La línea de trazos gruesos señala la termoclina.

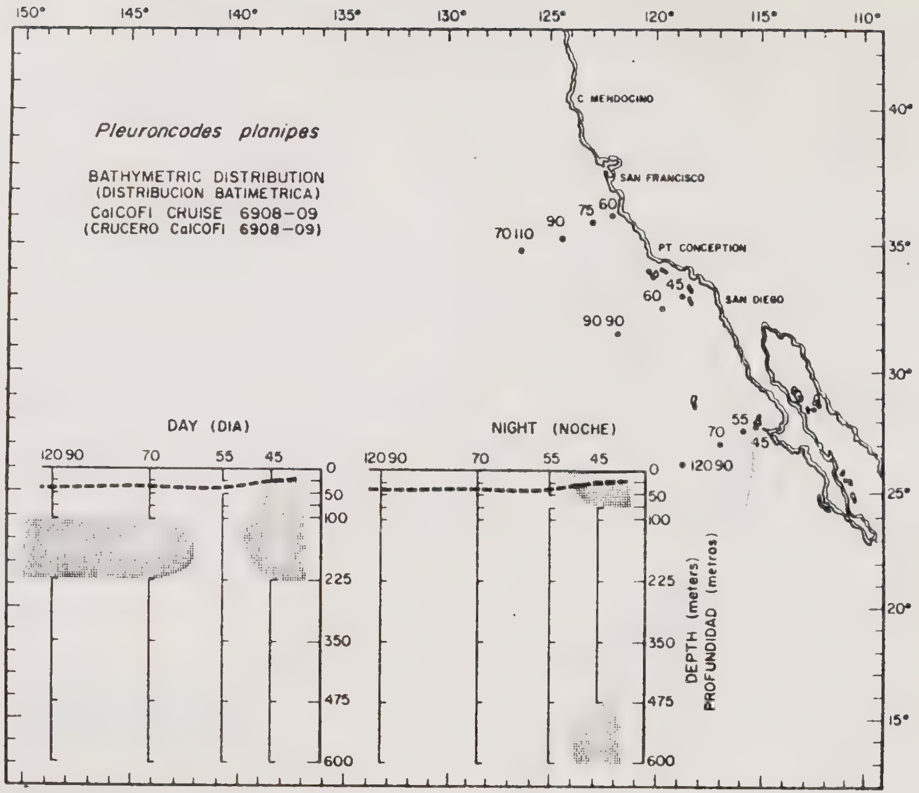
Pleuroncodes planipes
BATHYMETRIC DISTRIBUTION
(DISTRIBUCION BATIMETRICA)
CalCOFI CRUISE 6908-09
(CRUCERO CalCOFI 6908-09)
150°
145°
140°
135°
130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
15°
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
70 110
90
75
60
45
60
90 90
55
70
45
120 90
DAY (DIA)
NIGHT (NOCHE)
120 90
70
55
45
0
50
100
225
350
475
600
DEPTH (meters)
PROFUNDIDAD (metros)

Figura 3

Distribución batimétrica diurna y nocturna de Pleuroncodes planipes en aguas de California, durante el Verano, Crucero Agosto-Septiembre de 1969 (6908-09). Zonas sombreadas indican la distribución de este Galateido. Líneas verticales muestran las pescas en que la especie no aparecía. La línea de trazos gruesos señala la termoclina.

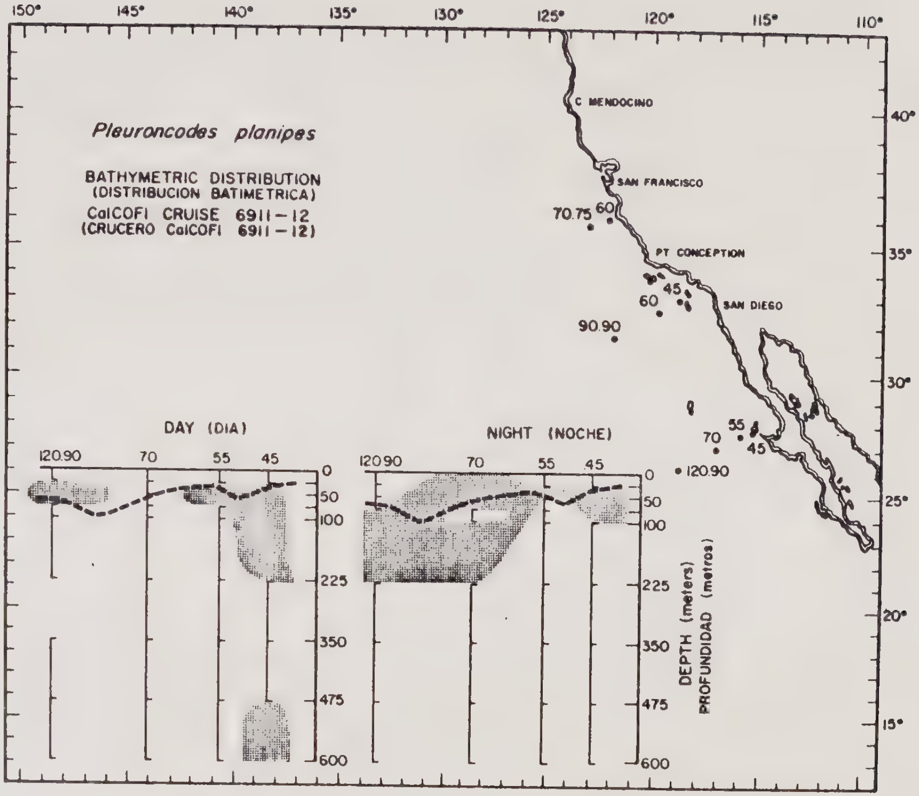
Pleuroncodes planipes
BATHYMETRIC DISTRIBUTION
(DISTRIBUCION BATIMETRICA)
CalCOFI CRUISE 6911-12
(CRUCERO CalCOFI 6911-12)
150°
145°
140°
135°
130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
15°
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
70.75
60
45
60
90.90
55
70
45
120.90
DAY (DIA)
NIGHT (NOCHE)
120.90
70
55
45
0
50
100
225
350
475
600
DEPTH (meters)
PROFUNDIDAD (metros)

Figura 4

Distribución batimétrica diurna y nocturna de Pleuroncodes planipes en aguas de California, durante el Otoño, Crucero Noviembre-Diciembre de 1969 (6911-12). Zonas sombreadas - indican la distribución de este Galateido. Líneas verti-- cales muestran las pescas en que la especie no aparecía. La línea de trazos gruesos señala la termoclina.

7606

Memorias del Simposium sobre Recursos Pesqueros Masivos de México
Ensenada, B.C., del 28 al 30 de septiembre de 1976.

EL ZOOPLANCTON Y LA PESCA

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RESUMEN

El problema más crítico en las investigaciones de pesca consiste en determinar la magnitud de la población de nuevos reclutas que irán a integrarse a la población pesquera.

El grado de mortalidad más elevado en el ciclo vital de los organismos marinos corresponde a las fases tempranas de su existencia, que comprende los huevos y estados larvales.

La información que se incluye discute los efectos que producen los factores bióticos y abióticos en la vida de huevos y larvas de los organismos marinos. Los factores más importantes que influyen en la vida de las primeras fases larvales son, el alimento y la depredación, y así se analiza en particular el efecto que ejerce la depredación en la supervivencia de las larvas de peces y de otros animales de interés comercial, sobre todo cuando existe alimento suficiente y con las características requeridas para su subsistencia.

Se revisan los datos y la información pertinente que aparece en la literatura, en relación con las diversas especies de interés comercial y para distintas regiones oceánicas, estableciendo así que la merma que se observa en las poblaciones jóvenes está en relación con una abundancia de los organismos depredadores que concurren en la misma región.

Se establece en general, una comparación entre los tipos de pesca industrial y artesanal, y los efectos respectivos que producen en el equilibrio ecológico oceánico.

Es evidente que el estudio metódico y detallado del plancto es fundamental para encontrar las claves que servirán para determinar la progresión positiva o negativa de las pesquerías, ya que mediante el zooplancton se pueden detectar con precisión los cambios físico-químico-biológicos que se producen en las regiones oceánicas, para entonces analizar las interrelaciones que se producen entre dichos factores, y en consecuencia obtener información sobre los variados agentes que influyen en la magnitud que han de alcanzar las nuevas poblaciones de reclutas. Hasta que estos múltiples aspectos de la investigación no se completen y dominen en sus variadas interrelacionadas, no podremos tratar de predecir el efecto que producirán en las poblaciones pesqueras, y en consecuencia poder estimar la magnitud dela población disponible para la pesquería.

EL PLANCTON Y LA PESCA

Con objeto de evaluar la magnitud de las poblaciones de reclutas que - se integran a la pesquería, se precisa un acopio de datos que se refieren a los factores que afectan el grado de supervivencia de los integrantes de las generaciones jóvenes respectivas.

Joubin (1924) discutía el elevado valor de fecundidad que muestran los peces e indicaba: "mais tous ces petit poissons n'arrivent pas á leur état adult, leur destruction est intense et necessaire pour arriver á un équilibre entre la quantité de nourriture et le nombre de ceux qui la mangent."

Los peces marinos de importancia comercial ostentan una fecundidad extremadamente elevada, pero muchos huevos y larvas perecen y así se obtiene una cierta estabilidad en las poblaciones.

La mortalidad es más elevada durante los primeros meses de la vida del animal (Gulland, 1965, Lasker 1965, May, 1974) y por esta razón, los factores que producen la mortalidad de las larvas están íntimamente relacionados con los proglemas básicos de la dinámica de poblaciones.

Las investigaciones en relación con la abundancia de huevos y larvas se desarrollaron desde que Hensen (1887) ideó un método para estimar la magnitud de la población reproductora, mediante cálculos que se basaban en el número de huevos colectados en el mar, correspondientes a las distintas especies de peces, y relacionando estos valores con los correspondientes a la fecundidad de las hembras respectivas, para llegar así a calcular la población reproductora total. Es evidente que el número de huevos variará en proporción con la magnitud de la población adulta en una determinada región. Sin embargo, el número de huevos, larvas y juveniles que sobreviven varía en los distintos años, de tal modo que de una población reproductora numerosa pueden resultar pocos reclutas y viceversa. Ahlstrom (1966) basa sus cálculos en la población de larvas.

Todas estas observaciones han originado que se realizaran estudios sobre los factores que causan la muerte de huevos, larvas y juveniles de los peces y otros animales marinos de interés comercial.

Gulland (1965) considera que es fundamental para determinar las poblaciones de peces, poder llegar a calcular con exactitud la mortalidad que se produce en las primeras fases de la vida, ya que precisamente en esa etapa del ciclo vital del pez es cuando se establece si la nueva generación será numerosa o pequeña, y ese período crítico de la vida del pez coincide precisamente con las primeras fases larvales. Diversos agentes y procesos oceánicos se han considerado responsables de la destrucción de huevos y larvas de peces. Así, la acción mecánica del oleaje destruye huevos y larvas pelágicos (Rollefsen, 1930, 1932; Devold, 1935; Zaisev, 1968; Pommeranz, 1974). La luz se considera perjudicial para los huevos demersales, como los de la platija, que incuban en zonas débilmente iluminadas (Hempel y Weikert, 1972; Pommeranz, 1974), y las radiaciones ultravioleta pueden afectar a los huevos pelágicos distribuidos por las capas oceánicas más superficiales (Marinaro y Bernard, 1966). El 99% de la mortalidad en las nuevas generaciones de Sardinops sagax se produce en el período que se extiende desde el huevo hasta la fase premetamórfica de la larva. Esto sugiere que determinado la mortalidad que se produce en ese período sería posible obtener estimaciones de la magnitud que alcanzaría la población recluta. Como se ha mencionado, la larva al nacer está expuesta a la acción de varios agentes, físicos, químicos, además del hambre, enfermedades y depredación. Las pérdidas que resultan por falta de alimento han de ser elevadas, ya que la diminuta larva requiere cantidades específicas de alimento, en cuanto al tamaño de la partícula alimenticia y su calidad nutritiva. Murphy (1961) considera que aunque el alimento sea un factor clave en la supervivencia de las larvas de peces, por lo que respecta a la Sardina de California, ese -- factor no desempeña al parecer, un papel determinante en la magnitud de las generaciones nuevas de sardinas, y así expone varios argumentos en apoyo de esta tesis. Blaxter y Hempel (1963) han observado en los estudios continuados que han venido realizando sobre los huevos de Clupea harengus, que los huevos grandes producen larvas más grandes, más fuertes y por lo tanto con mejores oportunidades para sobrevivir, que las que resultan de huevos pequeños. Ciemchomski (1966) ha observado en los experimentos de laboratorio, que la capacidad de supervivencia de las larvas de la anchoa argentina -- (Engraulis anchoita) no dependía del tamaño de los huevos; pero en una comunicación personal (1975) Ciemshomski manifestó que efectivamente las larvas procedentes de huevos grandes tenian mejores probabilidades de supervivencia que las larvas resultantes de huevos pequeños. Aquí hay que advertir, que en el laboratorio las larvas se mantenían en un ambiente propicio y con el alimento adecuado, y así hay que tener en cuenta que los resultados experimentales hay que interpretarlos comparándolos con el mundo real oceánico.

Blaxter y Hempel (1963) indican que las larvas de peces deben de disponer de alimento adecuado antes de que se reabsorba el saco vitelino, pués en caso contrario perecen, considerando este período, crítico en la vida del pez.

Hempel (1965) estipulaba que depredación y hambre son las dos causas -- principales de la mortalidad de larvas de peces. Sin embargo, se han dedicado más estudios a la alimentación, considerando que las larvas podían -- escapar eficientemente a la acción de los organismos depredadores, y consideraba que las pérdidas debidas a la depredación se podian determinar fácilmente estimando la abundancia de los organismos depredadores, pero sin tener en cuenta que la capacidad depredadora varía con las diferentes especies, ni tampoco incluía el concepto de la competición por alimento que se establece entre los zooplanctontes depredadores y las larvas. Hempel (1965) asumía que en muchos casos, los años que se caracterizan por una abundancia de organismos de presa son al mismo tiempo años ricos en alimento suficiente para nutrir larvas y depredadores planctónicos. Sin embargo, en es ta aserción no se considera la capacidad del depredador para seleccionar el alimento, siendo además obvio que los organismos depredadores, en el plancton, han de atacar y devorar más larvas de peces (fáciles de engullir y con mayor potencial proteíco) que por ejemplo a los crustáceos planctónicos. Aún cuando existe un buen número de publicaciones sobre el alimento planctónico de las larvas de peces, la mortalidad ocasionada por depredación no ha sido determinada, aún cuando este factor ha sido plenamente aceptado y discutido por los biólogos más prominentes, quienes consideran que las pérdidas de larvas que ocasiona la depredación son elevadas y en grado proporcional a la abundancia y categoría de los correspondientes de régimen carnívoro en el plancton.

Hay que considerar además que, cuando la cantidad y calidad de alimento disponible es adecuado para las larvas, su desarrollo es normal, y cuando el alimento escasea, las larvas se debilitan, resultando así más vulnerables a enfermedades y a la depredación. Hardy(1956) considera que una parte muy importante de las investigaciones pesqueras son las fluctuaciones en la respectiva abundancia que presentan los grupos de peces correspondientes a varias edades del ciclo vital respectivo. Se ha observado que en muchos casos la escasez de una generación particular no ha sido ocasionada por una disminución en la cantidad de adultos reproductores. La cantidad de alimento adecuado concurrente con la presencia de los alevines varía enormente en los distintos años. Sin embargo, la escasez de alimento no es el único peligro con que se enfrentan las larvas, ya que Medusas, Sifonóforos, Condróforos, Ctenóforos, Quetognatos, Poliquetos y otros zooplanctontes carnívoros imponen una tasa a la delicada población de larvas, y que además compiten con aquellos para obtener alimento. Durante algunos años esos voraces animales aparecen en cantidades considerables, y los efectos que producen, crean ciertas situaciones en el balance ecológico del reino del plancton.

De modo que, según se ha expuesto anteriormente, la magnitud de la población recluta estará delimitada en cierto modo por la acción de muchas variables, incluyendo las características de la puesta (calidad y cantidad de huevos), el ambiente oceánico (efectos mecánicos relacionados con el embate del oleaje, corrientes que desplazan las larvas a zonas desfavorables para su desarrollo), los factores químicos como la salinidad, oxígeno, otros elementos y especies químicas y los contaminantes; las características físicas, como la temperatura, luz, así como los factores biológicos, alimento y depredadores.

La temperatura del mar, afecta a los huevos durante el período de incubación y larval del saco vitelino, resultando crítica para el desarrollo, ya que modifica la actividad metabólica del animal, y por lo tanto la duración de las fases larvales (período más vulnerable en el ciclo vital del pez), y como resultado en la eventual supervivencia alcanzada durante dichas fases.

Como se ha venido exponiendo, las larvas de los peces resultan destruídas por diversos agentes, pero hay que singularizar que la depredación ocasiona la destrucción de una cantidad muy elevada de larvas (Lebour, 1922, 1923, 1925; Bigelow, 1926; Murphy, 1961; Hempei, 1965; Fraser 1969; Dekhnik et al, 1970; Alvariño, 1975, 1976, y muchos otros autores) han discutido este punto según se presenta a continuación.

Como se ha indicado, el problema más crítico en la investigación pesquera es poder determinar la población de nuevos reclutas que van a integrarse a la población pesquera. La información que se ha encontrado demuestra que existen muchos factores que controlan la supervivencia de huevos, larvas y juveniles y que las eventualidades por que pasan esas fases determinan la magnitud de la población resultante. De ahí que, el estudio de los factores que afectan la vida de la población durante aquel período resulta ser de importancia primordial. La mayor parte de los factores mencionados han sido analizados independientemente y en relación con la magnitud de la generación joven. Sin embargo, ninguno de esos factores bióticos y abióticos, independientemente considerados, han resuelto el problema. La solución está en el análisis combinado de la interacción intrincada de todos esos factores que afectan al futuro de la generación pesquera.

Al considerar los resultados obtenidos con los distintos estudios y las implicaciones en relación con los factores que actuan sobre la vida del pez, aparece evidente que las principales causas de mortalidad en las larvas son, falta de alimento y depredación, factores que a su vez entran en acción con los demás que determinan el futuro de la generación de peces. La muerte por inanición no se manifiesta con fácil evidencia en el océano (habría que realizar estudios histológicos en cada ejemplar para detectarla), pero sin embargo, depredación es un fenómeno bien visible, que se reconoce con toda su realidad en el océano, y ha sido observado miríadas de veces por los planctólogos al analizar las colecciones de plancton, ya que larvas de peces pueden verse fácilmente en el tubo digestivo de los depredadores. Sin embargo, a pesar de este hecho real y evidente, bien conocido de los planctólogos, estudios relacionados con la falta de alimento se han desarrollado repetidamente, aceptando que ahí residía la clave para determinar la mortalidad, mientras que los estudios para medir la intensidad y extensión de la depredación (un hecho plenamente observado y real) ha sido ignorado, deshechado y ni considerado por los biológos estrictamente pesqueros.

Por lo tanto, es muy sorprendente encontrar muy poca información sobre las actividades depredadoras de los organismos del plancton, y lo que se -- conoce sobre este tema parece disperso en la literatura, donde la mayor -- parte de la información pertinente abarca sólo unas líneas que aparecen en trabajos que no tratan específicamente sobre depredación.

Ha sido ignorada la importancia muy probable que tiene el factor depredación en larvas de peces, indican Lillelund y Lasker (1971) en la magnitud de la nueva generación resultante. Murphy (1961) considera que las larvas de peces sufrirán la misma acción depredadora que los otros organismos del plancton que presentan dimensiones similares y un comportamiento también semejante. Por lo tanto, la depredación puede ser un factor importante en el estudio de las poblaciones pesqueras, particularmente si el alimento disponible no resulta ser un factor limitante de la supervivencia, según expone Murphy, lo cual incluye también a las especies con valores de fecundidad muy elevados. Murphy (1961) indica que la depredación que ocurre en la comunidad planctónica de la región de California ha de ser responsable, al menos en parte, del rápido descenso en el número de larvas de sardina, y las variaciones en la depredación son principalmente responsables por las variaciones que se presentan en los valores de supervivencia que alcanzan las larvas correspondientes. La estructura más notable en la región de California es la Corriente de California, la cual produce variaciones en la temperatura oceánica, así como en la cantidad y calidad del complejo faunístico distribuido por esta región (Alvariño , 1966). Los datos históricos que se han ido recopilando señalan que durante los años cálidos se producen generaciones más abundantes de sardina que en los años fríos. Es cierto que las temperaturas bajas prolongan el período larval y por lo tanto la vulnerabilidad de las larvas, pero además el complejo faunistíco de los distintos año en relación con las características de la Corriente de California es también muy distinto, ya que en los años fríos, las poblaciones de zooplanctontes son más numerosas e incluyen especies depredadoras de mayor talla, que durante los años cálidos (Alvariño, 1966). Se han relacionado los volúmenes de plancton con generaciones de anchoas buenas y pobres. En el diagrama de la Fig. 1,se incluyen los volúmenes de plancton y el promedio de abundancia de Quetognatos para los años 1954 y 1958, observándose que en general, volúmenes elevados de zooplancton corresponden a concentraciones bajas de Quetognatos (activos depredadores en el plancton) y viceversa, con lo cual queda expresada así mismo la relación inversa entre el número de depredadores y la abundancia en las poblaciones de anchovetas.

Strasburg (1960) refiriéndose a las larvas de atunes, que incluían las de lista y de rabil (*Katsuwonus pelamis* y *Thunnus albacares*) y los volúmenes de plancton, señala que, cantidades elevadas de larvas de atunes coincidan con volúmenes de plancton medianos o reducidos, y las capturas de plancton mínimas y máximas contenían pocas larvas. Esta comparación es en cierto modo equívoca, ya que la notación volúmen de plancton es una magnitud que no proporciona información alguna de valor biológico. Es preciso conocer a los organismos que integran ese volúmen de plancton y la cantidad en que aparece cada una de las especies planctónicas en tales volúmenes. Así, cuando existía una elevada cantidad de zooplanctontes, como señala Strasburg (1969) coincidiendo con escasez de larvas, podría considerarse indicio de que los depredadores aparecían abundantes en el plancton y devoraban las larvas, y pequeños volúmenes de plancton con abundancia de larvas implicaría que el plancton estaba constituído casi exclusivamente por organismos que servían de alimento a las larvas y muy pocas o ningún organismo depredador. Los estudios de Stevenson (1962) que abarcan desde 1947 hasta 1951 en relación con la supervivencia de las larvas de arenque del Pacífico, Clupea pallasi, de la Columbia Británica (Canadá) indican que aún cuando se observaba la pérdida de larvas ocasionada por la depredación ejercida continuamente por Ctenóforos, Medusas y Quetognatos, no se efectuaron las consiguientes determinaciones (es decir, relacionando el número de individuos de presa para cada especie, su respectiva capacidad depredadora y co-ocurrencia con las larvas de arenque), pero también se había observado que existía una buena pérdida de larvas al ser arrastradas hacia mar abierto por las corrientes.

Harding y Talbot (1973) consideran en sus estudios sobre huevos y larvas de platija (Pleuronectes platessa) en la parte meridional del Mar del Norte, que aún cuando la mortalidad ocasionada por depredación no ha sido determinada, se acepta que debe ser elevada y que está en proporción directa con la abundancia de los organismos depredadores.

Ali Khan y Hempel (1974) comparan el plancton del Golfo de Adén con las larvas de peces capturados en aquella región, y han observado una relación inversa entre la cantidad de plancton y de larvas, aunque en este caso habría que estudiar con detalle el plancton presente en la localidad, es decir, analizar la proporción de especies que sirven de alimento a las larvas y las especies carnívoras.

Thayer et al. (1974) estudiando el plancton de la parte inferior del estuario del río Newport (Carolina del Norte) observaron que incluía abundantes copépodos (81% del total) acompañados de larvas de balanus y de otros crustáceos, y además aparecian cladóceros, ostrácodos y quetognatos. Estos autores observaron que ese plancton disminuía notablemente en la época en que las larvas de peces entraban en el estuario. Esta información demuestra una relación evidente entre las larvas de peces y su correspondiente alimento en el plancton.

Analizando los datos que presenta Russell (1933, 1935) se observa que la abundancia de larvas de peces coincidía con abundante alimento planctónico en la misma región, y la escasez de larvas correspondía con un elevado número de medusas, sifonóforos y ctenóforos en el plancton.

En la región de las islas Británicas existen dos especies de Quetognatos predominantes en el plancton, Sagitta setosa y S. elegans, y Russell en sus estudios ininterrumpidos en aquella región, ha demostrado que cuando S. elegans dominaba en el plancton coincidía con una cantidad elevada de larvas de peces, mientras que cuando la especie dominante era S. setosa las larvas de peces aparecían en cantidades reducidas. Al analizar los datos para todos los años estudiados se observa que las aguas caracterizadas por S. elegans contienen plancton rico en organismos que sirven de alimento a los peces (Copépodos y zoeas), y en las aguas típicas de S. setosa predominan las Medusas,Sifonóforos y Ctenóforos. Ahí tenemos de forma evidente el efecto que produce la abundancia de alimento y la concentración de depredadores en el plancton. Los estudios realizados por Russell (1934) sobre el zooplancton del Mar de Coral, indican que una elevada concentración de Quetognatos, Sifonóforos y Medusas coincidía en todos los casos con una escasez o una carencia total de larvas de peces. Lucas y Henderson (1936) notan que en aguas de Escocia no se efectuaban buenas capturas de arenque cuando se presentaba una elevada abundancia de Medusas. Russell (1970) menciona que la Medusa Cyanea se alimenta de larvas de langosta, y cuando dichas Medusas aparecen abundantes, generalmente después de cuatro años, escasean las langostas. Los Ctenóforos, principalmente Pleurobrachia, también se alimentan de larvas de moluscos, y así Kincaid (1915) y Nelson (1925) han observado en las costas de Washington una correlación inversa entre la progresión de los bancos de ostras y la abundancia de Ctenóforos en el plancton. También la Medusa Aurelia aurita ataca a las larvas de ostras (Orton, 1922), y así cuando cualquiera de esos animales abundan durante la época de reproducción de las ostras el número de individuos que se integran a la población adulta disminuye notablemente.

Durante el período 1966-1967 se observó Cort y Pérez-Gándaras,1973) que Octopus vulgaris, Loligo vulgaris y Sepia officinalis hierredda aparecían en enormes cantidades en el Banco Sahara (23°N -25°N, frente al Sahara Español), zona en donde se había practicado una pesca intensiva por espacio de varios años de Spáridos abundantes en aquellas regiones. Al mismo tiempo que los Cefalópodos aumentaban, las especies de Sparidos, Dentex-dentex, D. canariensis, Pagrus pagrus y otros, que usualmente eran abundantes en esta zona, habian disminuído notablemente, y se relacionó directamente la escasez de Sparidos con la pesca excesiva que se habia desarrollado en aquellos parajes. Sin embargo, como se ha indicado, la disminución - en las poblaciones de Spáridos, coincidía con una superabundancia de Cefalópodos. Al analizar el plancton de la región del Banco Sahara, se observó que las larvas de Spáridos parecían devoradas por los Cefalópodos, y las larvas de éstos, que normalmente servían de alimento a los Spáridos, carecían de enemigos, al disminuir la población de peces adultos, y como resultado de la escasez de Spáridos, depredadores en los Cefalópodos, estas poblaciones progresaron en su desarrollo sin competidores ni enemigos, mientras que los peces no podían recuperarse de la esquilmación debida a la -- acción depredadora y la pesca. En esta situación se reconoce el resultado producido por dos agentes, principalmente, depredación y pesca monoespecífica o restringida a un sólo grupo de peces. Con objeto de remediar la situación creada inicialmente por la pesca, al ser ejercida sobre un sólo grupo de organismos, se procuró desarrollar una pesca intensiva de Cefalópodos en la región del Banco Sahara, tratando de equilibrar aquel complejo faunístico.

Lo que se acaba de exponer, es un ejemplo del desequilibrio ecológico producido por una pesca singularizada o estrictamente aplicada a un grupo de peces. Así en las dos principales categorías en que se divide la práctica de la pesca, industrial (monoespecífica) y la artesanal que abarca la pluralidad de especies marinas pertenecientes a varios grupos zoológicos, aquélla va progresivamente mermando la población, ya que la industria selecciona una especie y realiza capturas exhaustivas, llegando así a producir un desequilibrio catastrófico en el ambiente oceánico. En el caso de la pesca del camarón, por ejemplo, en los lances comerciales hay muchos peces y otros crustáceos no se aprovechan (Chapa, 1976) y se devuelven al mar, así se ha observado que mientras las especies de camarón han disminuido en pocos años de 35.37% al 8.9%, la fauna de acompañamiento (peces y otros crustáceos,equinodermos etc.) ha aumentado del 64.62% al 91.06%.

Sin embargo, la práctica de la pesca artesanal,con su diversificación, mantiene en un cierto grado el equilibrio natural oceánico. Esta es la pesca que abarca Crustáceos, Moluscos, Peces, mediante la cual se obtienen las especies más apreciadas en el consumo de los restaurantes de más renombre por el selecto y exquisito menú que presentan al público. Esta pesca mantiene además pueblos y familias, que no sólo obtienen de la pesca su alimento básico y sus ingresos monetarios, sino que combinan esta ocupación con otros menesteres, como la agricultura, ganadería y otras ocupaciones, manteniendo así su economía también diversificada.

Todo lo expuesto coincide con las ideas de Graham (1943) al indicar que, una administración inteligente y sensata de las pesquerías debe operar de acuerdo con los procesos naturales del océano. Hardy (1956) explica que en el estudio metódico y detallado del plancton, principalmente del zooplancton incluyendo el ictioplancton, se asientan importantes claves para comprender mejor el éxito y fracaso de las pesquerías. Así mismo, con el estudio de las fluctuaciones correspondientes a períodos amplios y cortos en la abundancia y distribución de los zooplanctontes, se obtendrá información valiosa para detectar y analizar los cambios físico-químico-biológicos en el océano, y como consecuencia se llegará a un conocimiento más completo en lo que respecta a los recursos pesqueros, al reconocer el efecto que producen todos aquellos agentes en el medio oceánico. De esa forma se podrá determinar con la requerida exactitud, la magnitud de la población de reclutas que se integra a la población pesquera.

Hasta que todos esos múltiples aspectos de la investigación no se completen y dominen en sus variadas interrelaciones, no podemos tratar de predecir el efecto que producen en la pesca los cambios que ocurren en dichas variables, y por lo tanto, llegar a determinar la magnitud de las poblaciones.

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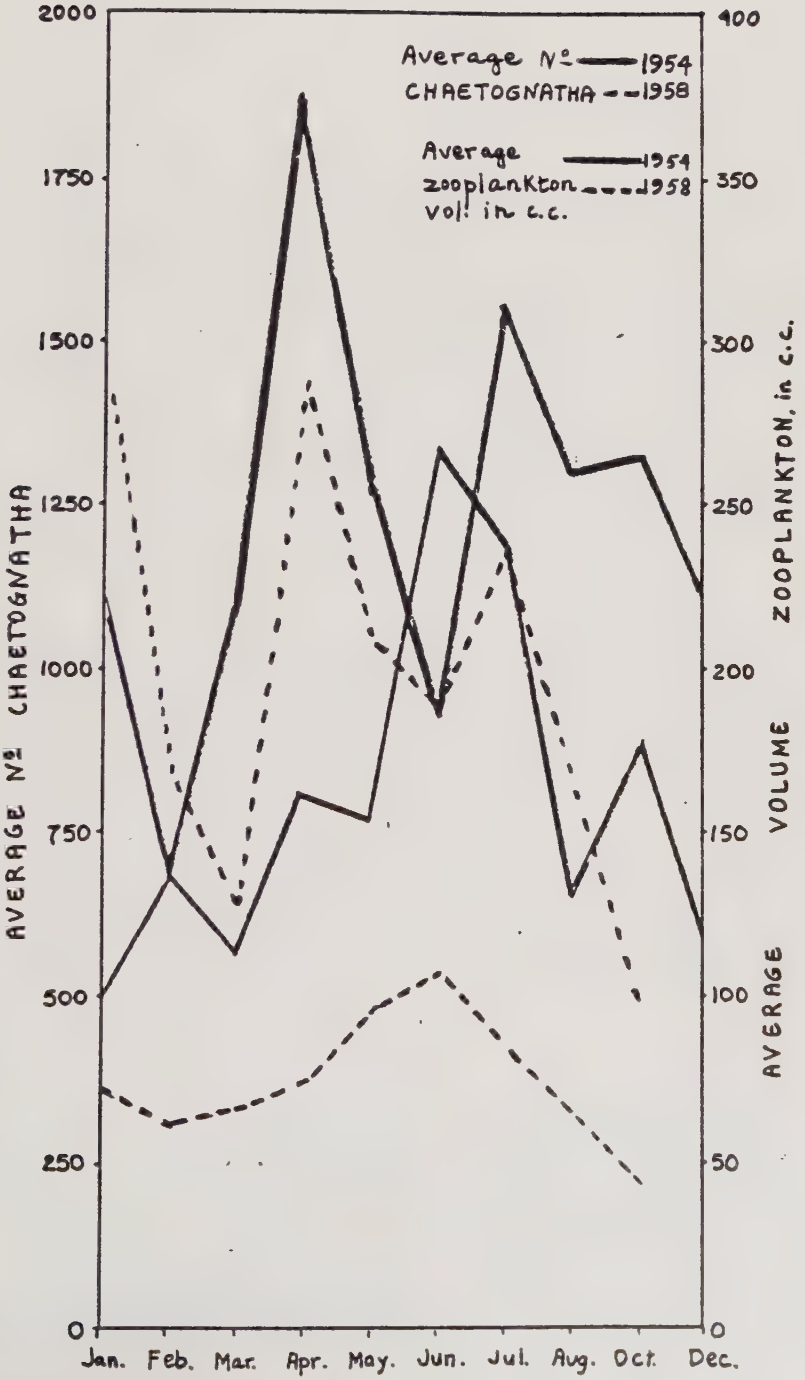
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Fig. 1

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FOOD AND FEEDING OF LARVAE OF THREE FISHES OCCURRING IN THE CALIFORNIA CURRENT, *SARDINOPS SAGAX*, *ENGRAULIS MORDAX*, AND *TRACHURUS SYMMETRICUS*[1]

DAVID K. ARTHUR[2]

ABSTRACT

The size, number, and types of food particles eaten by larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, were determined by an examination of gut contents of larvae captured in plankton samples from the California Current. Food particles found in larvae of the three fishes were predominantly the eggs, nauplii, and the copepodid stages of the smaller species of copepods. These increased in width as the larvae grew though not so uniformly for the anchovy as for sardine and jack mackerel. Particles ingested by anchovies at first feeding were slightly larger than were those ingested by sardines, while jack mackerel could eat particles three times wider than sardines of equal length. The smallest individuals of each species were the most euryphagous, especially anchovies. Feeding incidence of sardine and anchovy declined during the early larval period while that of jack mackerel increased. Sardine and anchovy larvae fed only during the day. The data were not analyzed for day-night feeding for jack mackerel.

The relative body depth and relative weight of laboratory-grown anchovy larvae increased throughout the larval periods examined, whereas, the relative body depth of most ocean-caught anchovy larvae decreased during the first half of this period, possibly as a result of the poorer ration obtainable in the ocean. The decline in relative body depth of ocean-caught anchovy larvae may be related to the decline in feeding incidence and to the apparent lack of increase in size of the food particles ingested.

Owing to the impending collapse of the Pacific sardine, *Sardinops sagax*, fishery, a biological-oceanographic survey program, which later became known as the California Cooperative Oceanic Fisheries Investigation (CalCOFI), was initiated in March 1949. Instrumental in initiating a program to study the food of the sardine larva was the concept developed by Hjort (1914) that the success of a year's spawning may be determined at the critical period when the fragile larvae must secure sufficient food from their environment. For a recent and thorough review of the literature concerning this subject, the reader is directed to May (1974).

To explore the possibilities proposed by Hjort (1914), 10,408 sardine larvae from 398 samples were examined. Food of two potential competitors, namely the northern anchovy (*Engraulis mordax*, 2,350 specimens, 69 samples) and the jack mackerel (*Trachurus symmetricus*, 750 specimens, 65 samples) was also investigated (Arthur 1956). Larvae of these three fishes were supplied to me by Elbert H. Ahlstrom and came from samples taken during early years of the CalCOFI program.

Sardines no longer support a viable fishery, but anchovies have increased in numbers to fill, in part, the ecologic if not economic void. Increasing attention, therefore, will be paid in this paper to this fish and to other species of the genus *Engraulis* which occupy coastal environments of many parts of the world (Reid 1967).

METHODS

Specimens were examined in glycerin because of its advantages over water. Its clearing qualities aid in the detection of food particles within the gut, and the greater viscosity of this medium dampens the movement of particles during dissection. Also, when in glycerin, larvae seem to be more pliable and the intestinal walls do not tend to fragment so readily.

At first the entire intestinal tract of each sardine larva was dissected from the body. This

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[1] Based on a portion of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree at the University of California, Scripps Institution of Oceanography.

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procedure proved to be difficult, unnecessary, and, at times, actually misleading. It was unnecessary because no food was ever found in the thin walled anterior intestine which forms about half of the total length of the digestive tract. Also, to view the anterior intestine, the liver which surrounds most of it must be carefully teased away resulting in the production of many fragments which may be confused with possible food particles. Schumann (1965) observed that food particles pass through this portion of the gut in about 25 s in laboratory-reared sardine larvae. The intestines of jack mackerel larvae are not as readily observable as in sardine or anchovy larvae because they are covered by well-developed pelvic fins and because of the earlier development of substantial body walls.

The presence of a single food particle in larval sardines or anchovies can usually be detected by a localized swelling of the surrounding gut wall. When several food particles are present, the posterior intestine may be highly expanded over its entire length. Food particles were dissected out of the gut by means of an instrument consisting of a pig's eyelash, bevelled cut to form a chisel point, and mounted in beeswax in one end of a glass tube. Food particles were identified to taxa as far as their condition allowed.

Each organism found in the intestine was measured as to the maximum cross section that the larva would have to encompass for ingestion. Herring larvae have been shown to ingest crustacean food particles "head on" by Hardy (1924), Bowers and Williamson (1951), and Blaxter (1965). This maximizes the ingestible size of the organism and positions appendages, spines, and setae to the rear of the food organism during its transit through the intestines.

To facilitate a consideration of changes in food with respect to growth, the size ranges of larvae of each of the three species of fishes being considered here have been subdivided into three length groups. The length intervals used in these subdivisions are based on the distribution of sizes in the collections rather than on any definite changes in the larvae with respect to age.

FOOD OF SARDINE LARVAE

Type of Food

The qualitative results of the examination of food material from intestines of larval sardines are presented in Table 1. Length of sardine larvae at the end of the yolk-sac stage is variable. One as small as 3.4 mm contained food, others as long as 5.5 mm still had yolk, but no larva was observed containing both yolk and ingested food organisms. Eggs, nauplii, and juvenile stages of copepods composed almost all of the identifiable food. Copepodid stages in the diet increased in percentage by a factor of 100 through the successive size groups of the larvae. This is undoubtedly due to the severe size restrictions placed on the young larva by the small size of its mouth. As the larva increased in size, its mouth likewise increased in gape, and consequently a larger range of the size spectrum of plankton became available.

TABLE 1.–Food of sardine larvae.

	Size group					
	End of yolk-sac stage to 5.5 mm		6.0 to 9.5 mm		10.0 to 25 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs	141	22.0	35	10.8	10	28.6
Copepod nauplii:						
Calanoid	40		18		3	
Cyclopoid	68		39		3	
Harpacticoid	62		42		2	
Unidentified	179		149		5	
Total nauplii	349	54.5	248	76.3	13	37.1
Copepodid stages:						
Calanoid			1		7	
Cyclopoid	2		7		3	
Harpacticoid			2		1	
Unidentified			1			
Total copepodids	2	0.3	11	3.4	11	31.4
Dinoflagellates	5	0.8				
Tintinnids	20	3.1				
Foraminifera	3	0.5				
Unidentified crustacean eggs					1	2.9
Unidentifiable material	120	18.8	31	9.5		
Total number of food particles	640		325		35	

Size of Food

Although they are not always of the largest ingestible size, the food particles increased in size isometrically with the increased length of sardine larvae (Figure 1). A larva in doubling its length from 4 to 8 mm likewise doubled its maximum ingestible food size from 80 to 160 μm.

Feeding Incidence

The percentage of fish containing at least one food particle is termed the "feeding incidence" for

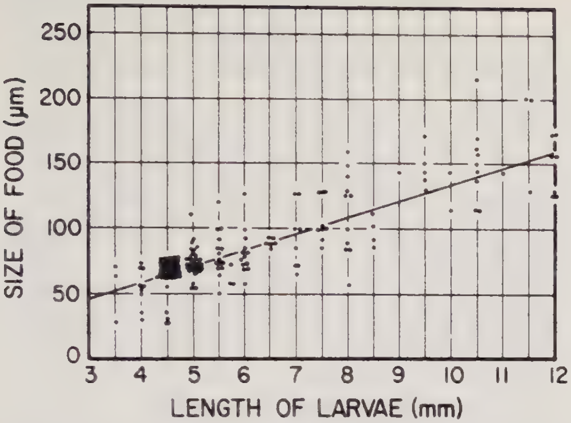

FIGURE 1.–Food size of Pacific sardine larvae. The line is a least squares fit to all data points and is expressed by the equation: $\hat{S} = 13.04L + 5.70$, where $\hat{S}$ is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.813 and the coefficient of determination r^2 implies that 66% of the variation in food size can be explained by larval size alone.

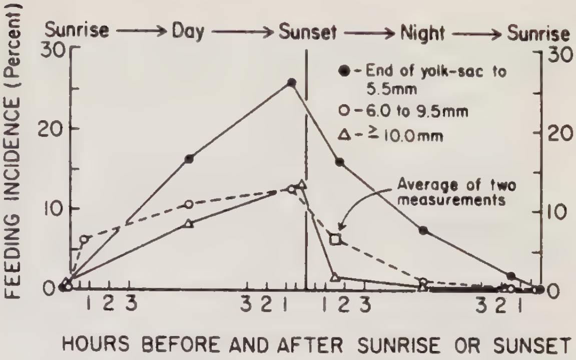

FIGURE 2.–Diurnality of feeding incidence of Pacific sardine larvae. Only those intervals in which at least 50 larvae coming from at least 5 samples are included.

a particular sample and is considered a measure of a larva's ability to obtain food in the environmental circumstances at the time of sampling.

The available data permit an inspection of the average hour-by-hour series of trophic events for sardine larvae (Figure 2). The data were divided into 16 intervals composed of: the first half hour, the second half hour, the second hour, and the third hour both before and after sunrise, and both before and after sunset. There were also midday and midnight intervals which vary in length according to the season. Only those intervals in which at least 50 larvae from at least five samples were included. Feeding incidence of all three size groups increased throughout the day. This could have resulted from accumulation of food in the gut, or perhaps to the success of larvae in finding more suitable feeding conditions as the day progressed. The largest size group demonstrated the fastest return to a low feeding incidence at night which probably reflects faster digestive rates for older larvae, as has been shown for plaice larvae (Yasunaga 1971). The lower feeding incidence of older larvae may, therefore, be partly due to an increased digestive rate.

Figure 2 illustrates the diurnal nature of feeding which is due to the visual feeding sardine larva requiring light to detect its prey. (Schumann 1965). This results in diurnal changes of the intestine. The posterior intestine of larvae captured during the early morning is visibly striated. In late afternoon and early evening, the posterior intestines of many larvae, especially the smaller ones, are expanded and have no visible striations. The intestinal wall contains large vacuoles of clear fluids. During this period of the day, it is common to capture larvae with greatly expanded intestines but with no identifiable food organisms. Often such larvae contain some granular material floating about in the intestinal lumen which is comparatively large due to the expansion of the surrounding wall. During the night, intestinal expansions disappear and by sunrise almost all of the larvae have returned to the compact, striated intestinal condition. This rhythm is most pronounced in the smallest size group where, as indicated in Figure 2, the amplitude of the diurnal feeding incidence is at a maximum.

FOOD OF ANCHOVY LARVAE

Type of Food

No larva was found containing both yolk and ingested food. The diet of anchovy larvae (Table 2) is very similar to that of the sardine. The most striking difference is that very young anchovies are more euryphagous. About 40% of their diet (by numbers) consists of noncrustacean food particles. A food category entitled "unidentified spheres" is represented by small (about 20 µm) objects, probably of plant origin. Copepod nauplii become increasingly important as anchovy larvae increase in length and compose the bulk of particulate food when all sizes of larvae are considered.

Copepod eggs and nauplii were found to be the most important element in the diet of larvae of

TABLE 2.–Food of northern anchovy larvae.

	Size group					
	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 9.0 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs	15	15.3	4	14.3		
Copepod nauplii:						
Calanoid	10		6		3	
Cyclopoid	13		11		6	
Harpacticoid	4		1		1	
Unrecognizable	15		1			
Total nauplii	42	42.9	19	67.9	10	90.9
Copepod adults:						
Calanoid					1	9.1
Clam larvae	2	2.0				
Foraminifera	2	2.0				
Tintinnids	3	3.1				
Dinoflagellates	7	7.1	1	3.6		
Ciliates	2	2.0	2	7.1		
Coccolithophores	4	4.1				
Unidentified spheres	21	21.4	2	7.1		
TOTAL	98		28		11	

Engraulis mordax (Berner 1959), of *E. anchoita* (Ciechomski 1967), and *E. ringens* (Rojas de Mendiola 1974). Berner and Rojas de Mendiola found considerably more eggs than nauplii while Ciechomski reported about equal numbers.

An unusual example of feeding by both anchovy and sardine larvae was called to my attention by Elbert H. Ahlstrom because of the obvious gorged intestines of some of the larvae. This sample was taken about 38 km off the coast of central Baja California approximately 6 h after sunset and 1½ h after setting of a "first quarter" moon. Unusual aspects of the sample were that most of the larger larvae of the two species contained food at night and that they were literally crammed with the pteropod *Limacina bulminoides*. Of the larvae over 10 mm in length, the 26 feeding sardines averaged 24 pteropods per gut with a maximum of 54 in one 23-mm larva, and the 19 feeding anchovies averaged 18 per gut with a maximum of 26 in a 14-mm individual. Compared to the one or two food particles usually found in a feeding anchovy or sardine larva, the number of pteropods was surprising. The only other molluscs found in either sardine or anchovy larvae in this investigation were two bivalve larvae, one each in two very young anchovies. No molluscs were reported in the extensive investigations of the food of anchovy larvae by Berner (1959), Ciechomski (1967), or Rojas de Mendiola (1974). It cannot be determined whether the larvae found filled with *Limacina* reflected beneficial feeding conditions where they were found, or a hazardous situation in which the larvae had ingested material they could not digest and void.

Because the number of pteropods found in this one sample is larger than the total number of food particles found in the larger sardine and anchovy larvae of all other samples examined, they were not included in the overall tabulations for these fish. The size of the pteropods was used to establish the upper ingestible size of food particles for older anchovies (Figure 3a).

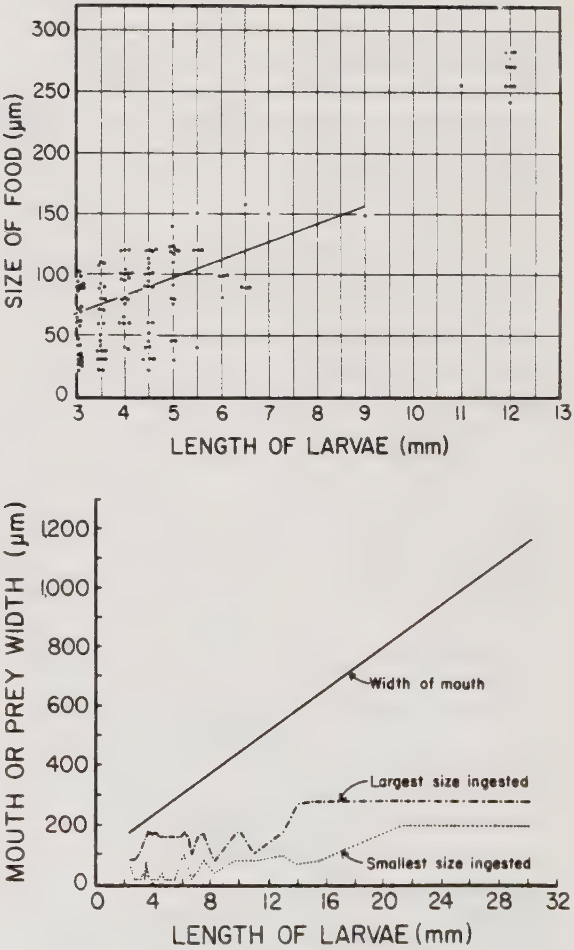

FIGURE 3.–(a) Food size of northern anchovy larvae. The line is a least square fit to all data points from 3 to 9 mm inclusive and is expressed by the equation: $\hat{S} = 16.16L$, where $\hat{S}$ is width of food in microns and L is standard length of larvae in millimeters. The correlation coefficient r is 0.473 and the coefficient of the determination r^2 implies that 22% of the variation in food size can be explained by larval size alone. (b) Food size of anchoveta (*Engraulis ringens*) larvae. Adapted from Rojas de Mendiola (1974).

Size of Food

Food particles of young anchovy larvae are not selected from those near the largest ingestible size as are those of young sardine larvae, though there is a trend to increase particle size as larvae increase in length. The correlation coefficients (Figures 1, 3a) suggest that food size of sardines is more controlled by larval size (0.813^2 or 66% of variance explained) than of anchovies (0.473^2 or 22% of variance explained). The extensive data, including many older larvae, reported by Ciechomski (1967) and Rojas de Mendolia (1974) indicate a sharp increase in food size between the larval lengths of about 3 to 4 mm but relatively little increase for most of the remainder of the larval period. Rojas de Mendiola's data (Figure 3b), including food sizes of 2,088 feeding larvae 3.1 to 5.0 mm in length, are used to illustrate this important point. These data indicate that food size roughly doubles (from approximately 100 to 200 μm) while larvae grew from 4 to 16 mm. Assuming that both larvae and food particles increased in size isometrically, then their volumes increased by the cube of their increase in length or width. Food particles in doubling in width increased 8 times in volume, while larvae increasing 4 times in length increased 64 times in volume. Therefore, the nutritional equivalent of a 200-μm food particle to a 16-mm larva is only one-eight of that of a 100-μm particle to a 4-mm larva. Although Berner (1959) measured the length rather than the width of food particles and his data are not directly comparable, they do indicate that while anchovy larvae increased in length from 3 to 10 mm (an increase of 37 times in volume) their average food size increased from 68 to 128 μm (an increase of only 6⅔ times in volume).

Feeding Incidence

Anchovy larvae also are daytime feeders (Figure 4). The disparity between night and day values for feeding incidence is greater for anchovies than for sardines during their youngest larval stages. This difference perhaps is due to a faster digestive rate for the anchovy.

FOOD OF JACK MACKERAL LARVAE

Type of Food

The jack mackerel larva first starts to feed when it is about 3.25 mm long. By the end of the yolk-sac stage, the jack mackerel has attained a robustness which contrasts sharply with the slender early larval sardine or anchovy. Its body shape, in general, is more substantial and its mouth is proportionately larger. No jack mackerel larva was found with both yolk and ingested food organisms.

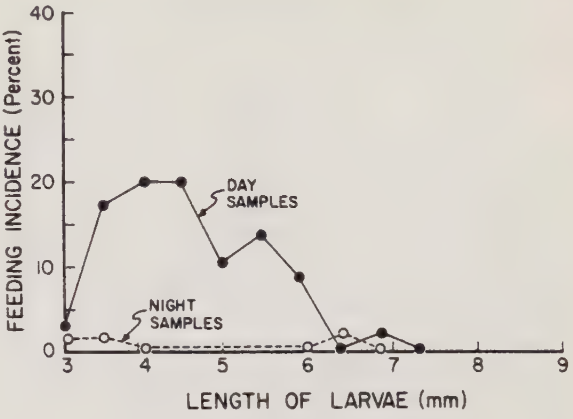

FIGURE 4.–Diurnality of feeding incidence of northern anchovy larvae.

Just as for sardine and anchovy larvae, copepods contributed the greatest bulk of its food (Table 3). Eggs and naupliar stages, however, are much less important. The "egg sacs," appearing under the title of copepod eggs, were probably ingested attached to adult copepods and so represented a coincidental fraction of the food. Copepod nauplii seemed to be significant in numbers only in larvae of the smallest size group.

Copepodid stages of copepods make up the bulk of particulate food, increasingly so as the larva grows older. By the time the larva is 7.0 mm long, 96.0% (by number) of its food is composed of various species of copepods. The most significant feature of the diet is the very high percentage of occurrence of *Microsetella norvegica*, one of the few planktonic species of harpacticoid copepods. This probably represents a definite selection, as this species of copepod, though ubiquitous, never achieved numerical importance in our plankton hauls. Jack mackerel (*Trachurus trachurus*) larvae were reported by Sinyukova (1964) to have an "inborn ability" to select two species of copepods from the mass of plankton living in the Black Sea. On the other hand, the respective behavior of the early jack mackerel larvae and *M. norvegica* may cause the two species to be locally aggregated, TABLE 3.–Food of jack mackerel larvae.

	Size group					
	End of yolk-sac stage to 4.5 mm		5.0 to 6.5 mm		7.0 to 10.5 mm	
Food items	No.	%	No.	%	No.	%
Copepod eggs:						
Single eggs	5	4.3	9	4.4		
Egg sacs	1	0.9	4	2.0	1	0.6
Copepod nauplii:						
Calanoid	3		3			
Cyclopoid	5		2		1	
Harpacticoid	7		2			
Total nauplii	15	12.8	7	3.4	1	0.6
Copepod adults:						
Calanoid:						
Calanoid spp.	7		15		60	
Metridia sp.	1					
Candacia sp.					1	
Cyclopoid:						
Oithona sp.	1				3	
Corycaeus sp.	3		3		5	
Oncaea sp.	6		29		39	
Harpacticoid:						
Microsetella norvegica	46		130		56	
Microsetella rosea	1					
Clytemnestra rostrata					1	
Unidentified					4	
Total copepods	65	55.6	117	86.3	169	96.0
Euphausiid:						
Nauplii	1	0.9			2	1.1
Calyptopi			2	1.0	1	0.6
Cladocera			1	0.5		
Unrecognizable crustacean remains	10	8.5				
Peteropods	3	2.6	4	2.0	2	1.1
Tintinnids	16	13.7	1	0.5		
Foraminifera	1	0.9				
Total number of food particles	117		205		176	

perhaps at the surface, thereby allowing the larva a disproportionate chance of securing individuals of this copepod.

Jack mackerel larvae may perceive food organisms by their color, since *M. norvegica*, and species belonging to the genera *Corycaeus* and *Oncaea*, are among the most brightly colored or least transparent of copepods. Species of the two latter genera also enter into the diet of jack mackerel larvae. Calanoid copepods become more important in the diet of larger larvae, perhaps because of an increased visual acuity, or their larger mouths, or a change in their vertical distribution. Whereas each feeding sardine or anchovy larva normally contains only one or two food particles, feeding jack mackerel larvae usually contain more. Some intestines contained *M. norvegica* in numbers as high as a dozen with no other observable food items.

Size of Food

The relatively large mouth of jack mackerel larvae is reflected in the larger food particles ingested (Figure 5). The preponderance in numbers of particles at a size of 120 μm (greatest cross-sectional dimension) is due to the apparent selection of *M. norvegica*. The gape of the larva apparently increases isometrically with increasing length of the larva. At 3.5 mm long, it can ingest particles up to 225 μm in cross section. Doubling its length to 7.0 mm also doubles its ingesting capacity to particles of about 435 μm in cross section.

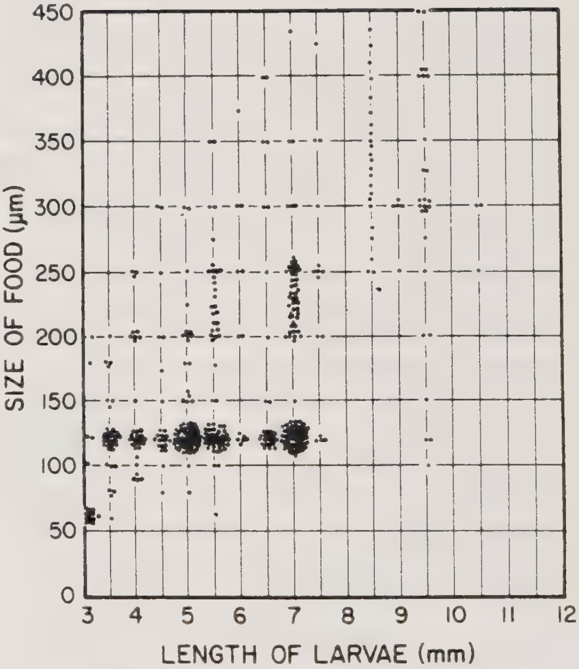

FIGURE 5.–Food size of jack mackerel larvae.

COMPARISONS

Type of Food

The three species may be characterized as primarily crustacean feeders as larvae (Table 4) and the youngest larvae are the most euryphagous. Crustacean food is predominant in all size groups of the larvae of all three species and, furthermore, becomes increasingly so as the larvae increase in size. Only in the smallest anchovies is noncrustacean food an important part of the diet.

TABLE 4.–Crustaceans as percentage of total number of identifiable food particles. Size groups of larvae–small = end of yolk-sac stage to 4.5 mm, middle = 5.0 to 6.5 mm, and large = 7.0 to 9.0 mm.

Species	Size group of larvae		
	Small (%)	Middle (%)	Large (%)
Sardine	96	100	100
Anchovy	58	82	100
Jack mackerel	83	98	99

Size of Food

Figure 6 compares the size ranges of food particles ingested by the three larvae. Because of their larger mouth, jack mackerel larvae can ingest particles about 3 times larger in diameter than can sardine larvae of the same length. This represents a difference in bulk of about 27 times between maximal ingestible sizes for the two larvae. The small anchovy can ingest particles about 40 to 50 μm larger than the maximum-sized particles of the sardine but does not appear to feed as frequently on organisms near to the maximum ingestible size as the sardine does.

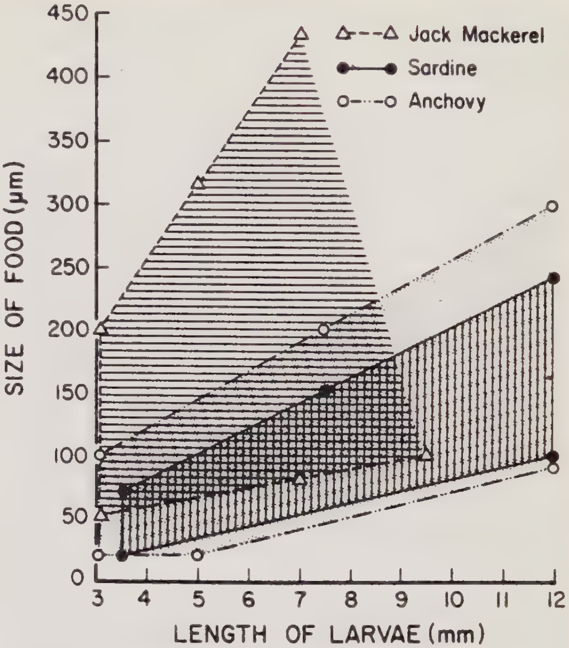

FIGURE 6.–Size range of food particles ingested by larvae of Pacific sardine, northern anchovy, and jack mackerel.

Feeding Incidence and Its Relation to Type of Intestine

Feeding incidence increases with length in the jack mackerel but decreases with length in the anchovy and sardine (Figure 7). The high percentage of jack mackerel larvae containing food may indicate that either they are more voracious feeders, or their digestive rate is slower, or perhaps they are less apt to void their guts while being caught and preserved. Feeding incidence of larval fish appears to be associated with the morphology of the gut. The intestine of the sardine and anchovy remains long and straight with little observable differentiation until the larva is about 20 to 25 mm long. On the other hand, when the jack mackerel has attained a length of about 4.25 mm, a portion of its gut forms a loop. This loop divides the larval gut into definite functional parts. Based on a long-range study of feeding habits of fish in the Black Sea, Duka (1967) classified the larval gut into three types: long straight, short straight, and looped. Duka noted also that larvae with looped guts usually contained much more food than larvae with straight guts. Ciechomski and Weiss (1974) noted that the feeding incidence of *E. anchoita* larvae (0-28.0%) was much lower than of hake larvae (63.3-94.5%) taken in the same plankton samples and that intestines of hake larvae are not straight but have several folds.

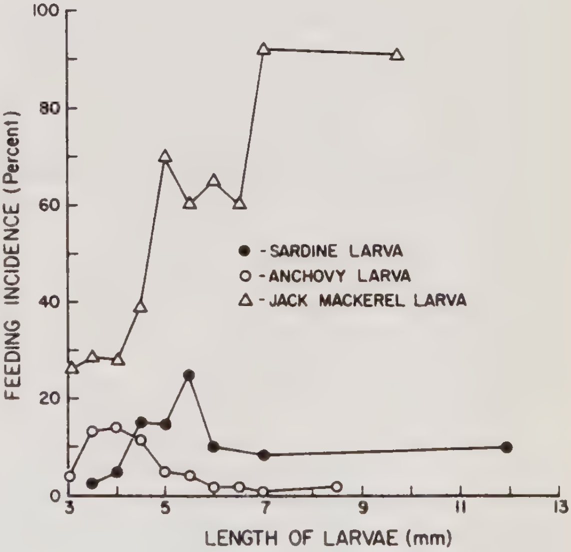

FIGURE 7.–Comparison of feeding incidence of Pacific sardine, northern anchovy, and jack mackerel larvae. Values for sardine and anchovy larvae are averages of day and night feeding incidences. Values for jack mackerel larvae are for all samples combined.

DISCUSSION

Significance of Feeding Incidence

For the past half century, there has been a discussion in progress concerning the significance of feeding incidence. Lebour (1921) called attention to the low feeding incidence of young clupeoids and attributed this to rapid digestion of food in the larval intestine. She was soon challenged by Hardy (1924) who, after observing herring larvae defecating after capture, assumed the low value to be an artifact produced by most larvae voiding their guts. The subject has attracted increasing interest recently. June and Carlson (1971) and Kjelson et al. (1975) observed older larvae of the menhaden, *Brevoortia tyrannus*, defecating after rough handling and fixation. Anchovy larvae have been observed defecating rotifers and *Gymnodinium* while being handled in the laboratory (John Hunter pers. commun.). *Gymnodinium* is eaten by *E. mordax* larvae in the laboratory (Lasker et al. 1970) and probably so in the ocean (Lasker 1975). Rotifers and the veligers of various species of molluscs in combination with *Gymnodinium* sustain anchovy larvae in the laboratory up to about 25 days of age (Lasker et al. 1970; Theilacker and McMaster 1971). Blaxter (1965), however, in attempts to assess the effect of Formalin[3] on food retention of herring larvae was able to demonstrate that only 10% of the larvae empty their guts due to Formalin fixation. Detwyler and Houde (1970) studying laboratory-grown larvae of scaled sardine *Harengula pensacolae*, and bay anchovy, *Anchoa, mitchilli*, found almost all of even the first feeding stages contained food after samples of them were taken from the plankton rich rearing tank and preserved in 5% Formalin. Feeding incidence of clupeoid larvae captured in plankton nets has been positively correlated with the availability of food by Pavlovskaia (1958), Nakai et al. (1966), Burdick (1969), Nakai et al. (1969), Bainbridge and Forsyth (1971), and Schnack (1974). Blaxter (1965) cited the wide variation and observed feeding incidence in the literature concerning herring larvae. I believe that much of the confusion has resulted from many authors failing to consider the time of day when larvae were caught (Figure 2) or the age of the larvae (Figure 4). When these variables are taken into account, a series of observations of feeding incidence can reveal valuable insights into the tropho-dynamics of larvae. Feeding incidence must be viewed only as an indicator of feeding success because of the errors likely to be produced by defecation or to the difficulty in detecting soft bodied items such as *Gymnodinium*.

Comparison of the feeding incidence in four species of *Engraulis* (Figure 8) shows an increase in feeding incidence over larval lengths of 3 to 4 mm. Following this relatively high incidence at 4 mm, there is a drastic drop in this value until lengths of about 7 or 8 mm are reached. The mean feeding incidences for the four curves in this length range are 7 times higher for the 4-mm than for the 8-mm larvae. Feeding incidence remains low but relatively constant over the length range from 8 mm to about 14 mm at which point it begins to increase steadily over the remainder of the larval period. The value for the 20-mm length of *E. ringens* is based on only 12 specimens and, therefore, is not as reliable as values for other lengths.

The available data for sardine larvae suggest the same U-shaped curve. When the values for the sardine (Figure 7) are compared to Figure 8 it is seen that feeding incidence in relation to size falls roughly between *E. ringens* and *E. anchoita*, except that the decrease at intermediate sizes is not as precipitous. Yamashita (1955) reported the following feeding incidence values for larval *Sardinops melanosticta*: for about 14 mm = 8%, 21 to 30 mm = 56%, and 31 to 40 mm = 81% . The upward trend of these data is similar to those of larger anchovy larvae; however, the values are not comparable because the time of day of sampling was not reported. It seems significant that the shape of the curves of the four anchovy species (Figure 8) are so uniform in their relation to each other. *Engraulis ringens* is considerably higher than all others (except for the value at 20 mm). This probably is related to the rich plankton conditions of its habitat.

Clupeoid larvae visually detect prey, approach it, and then strike from a characteristic S-shaped posture. Proficiency of capture increases with age as observed in the laboratory for the larvae of herring and pilchard (Blaxter and Staines 1971), sardine (Schumann 1965), and anchovy (Hunter 1972). These investigators also noted that the volume of water searched increases with larval age. Feeding incidence should, therefore, increase markedly with age. Why, then, does the observed feeding incidence drop so drastically for anchovy

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

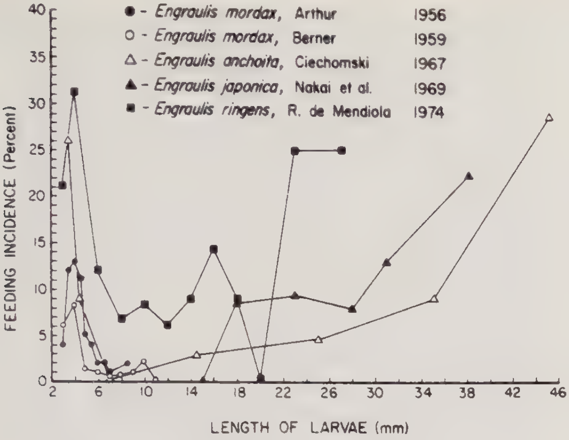

FIGURE 8.—Feeding incidence of larvae of various species of anchovy. Values are the average of day and night feeding (day values are divided by two because young anchovy larvae do not feed at night). Berner's data were recalculated to read "feeding incidence per length of larva" rather than "percent of feeding larvae occurring per length."

living in their natural environment? This could be partly a result of a faster digestive rate of older larvae as indicated for sardine larvae (Figure 2). It also could result if either the ambient food density decreases with time or the larval feeding activity decreases with age. There are reasons to suspect that both of these might occur and at the same time.

Decrease in Food Density

Sardine and anchovy larvae may initiate their first feeding in higher concentrations of food than they will experience several days later. Hand and Berner (1959) found that 74% of the food of adult sardines, when filter feeding at night, were small species of copepods, presumably the same species that produce the small nauplii so important in the diet of the sardine and anchovy larvae. Furthermore, they found that organisms in stomach contents had a high correlation with organisms in plankton samples taken at the same time and place. The adult anchovy, when feeding at night, is probably also a filter-feeding zooplanktivore although it does have more omnivorous tendencies (Loukashkin 1970), and the type of feeding, either biting or filtering, is controlled by the size of the food particles available (Leong and O'Connell 1969; O'Connell 1972). Both species also are selective feeders on larger organisms when visual conditions permit. As a consequence, filter-feeding adults by actively searching for rich feeding conditions for themselves also prospect areas suitable for their larvae. More sardine and anchovy larvae were shown to occur in samples where both species were collected than in hauls where they occurred alone (Ahlstrom 1967); he concluded that these samples were collected near centers of heavier spawning for both species. It would appear that spawning adults of the two species were seeking out the same conditions. Sardines (Ahlstrom 1954), northern anchovies (Bolin 1936), and Argentine and other anchovies (Ciechomski 1965) spawn at night. Both spawning and filter feeding take place at night; therefore, the eggs may be laid near concentrations of suitably sized copepods (assuming spawning and feeding occur on the same night). However, as soon as the eggs have been spawned, they begin to be dispersed by water movement from each other and from organisms they will need for food several days hence. Sardine eggs are spawned in dense patches according to Smith (1973), who calculated that the horizontal mean distance between nearest neighbor eggs is of the order of 1 to 2 cm at spawning and changes to 15- to 20-cm mean distance for several-day-old larvae. These larvae may experience a diminution of their early feeding conditions as a result of diffusion as well as of grazing by the various predators. These ideas are presented to suggest how a general dilution of the co-occurrence of egg and plankton patches could occur in time. Lasker (1975) has recorded how rich larval feeding conditions can be destroyed overnight by a single storm.

Condition of Ocean-Caught and Laboratory-Grown Anchovy Larvae

There are differences in physical condition of the average ocean-caught and laboratory-grown anchovy larvae. These differences are probably a result of the available food.

Ahlstrom et al.[4] have presented a series of measurements of anchovy larvae and juveniles taken randomly from samples of the CalCOFI program. Figure 9 is a scatter diagram of relative body depths (body depth measured just anterior to pectoral fin base ÷ standard length) calculated from the above date. This diagram demonstrates that relative body depths of ocean-caught anchovy

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[4] Ahlstrom, E. H., D. Kramer and R. C. Counts. Egg and larval development of the northern anchovy, *Engraulis mordax*. Unpubl. manusc.

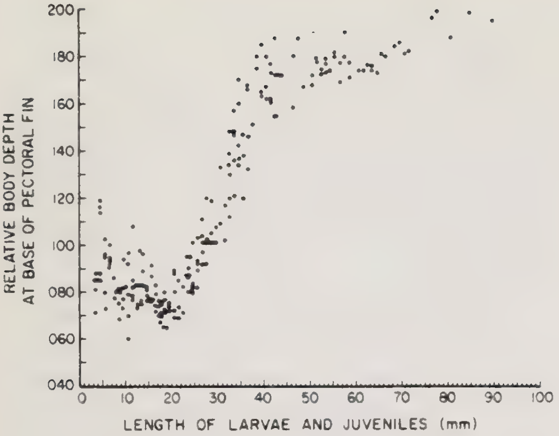

FIGURE 9.–Relative body depth of ocean caught northern anchovy larvae and juveniles calculated from Ahlstrom et al. (see text footnote 4).

larvae generally decrease until they are 17 to 18 mm long. Figure 10 compares relative body depth, averaged per millimeter of length, of the above ocean-caught anchovy larvae to that of larvae grown in the laboratory. These are larvae grown by Kramer and Zweifel (1970, experiment 17-II) at 17°C on a diet of wild plankton and with a feeding incidence described as "high." At the 10-mm length the two curves are different at the 0.05 significance level (*t*-test) and they differ with greater significance at increasing lengths.

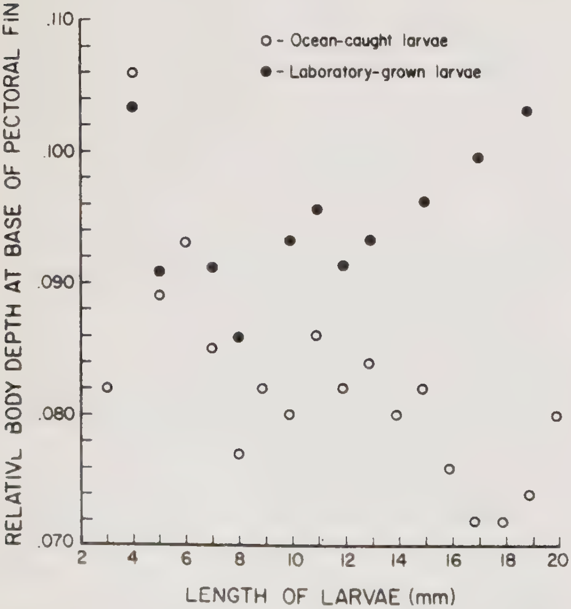

FIGURE 10.–Comparison of relative body depth of ocean caught and laboratory grown northern anchovy larvae. Each point represents an average of at least four larvae.

Condition factor (weight ÷ length^3) for laboratory-grown anchovies increases throughout the larval period as calculated from weight-length relationships presented by Lasker et al. (1970) and Hunter (1976).

Condition factor for ocean-caught *E. anchoita* larvae as calculated from wet weight data recorded by Ciechomski (1965) is at its lowest value between 15 and 20 mm.

The available data, therefore, indicate that relative body depths and weights of well-fed laboratory-grown anchovy larvae increase allometrically throughout the larval period, whereas these values for average ocean-caught larvae are at a low value at some midlarval period, followed by an increase through metamorphosis. This increase is probably related to the start of transformation to the juvenile stage but may also be accelerated by improving nutrition.

A relationship between gut thickness and feeding conditions was reported for ocean-caught larval sardine *Sardinops melanosticta* (Nakai 1960, 1962). The relationship of body depth to the nutritional level of fish larvae has been recorded for *E. japonicus* (Honjo et al. 1959; Nakai et al. 1969) together with relative body weight for herring larvae (Blaxter 1965, 1971). Blaxter attributed the low value of body weight for ocean-caught herring larvae to scarce plankton and to few feeding hours in the Clyde area at the time of sampling. The 14- to 15-mm long laboratory-grown herring larvae when deprived of food died at relative body weights that were higher than those of living ocean-caught individuals. This may be a result of the ocean-caught larvae having survived on suboptimal rations most of their existence whereas the laboratory-grown larvae had ample rations until the time they were suddenly deprived of food. The observed decrease in condition with size might also be an index of the increasing ability to resist starvation. The rich feeding conditions of successful laboratory-rearing experiments probably seldom obtain in the ocean (Lasker 1975; Hunter in press), and this may be reflected in the condition of the average ocean-caught larva.

The sardine larva initiates its first feeding activities in a nutritional deficit (Lasker 1962). This may also be indicated by the increasing thinness of the average ocean-caught *E. mordax* larva until about midway through its larval existence. Further research is required to determine if the decline in relative physical condition indicates a state of serious malnutrition and, if so, how far from the well-fed state can the condition of the individual vary without resulting in mortality. It is also possible that laboratory-reared larvae have abnormally large relative body depths.

Food Size, Feeding Incidence, and Condition of Anchovy Larvae

The foregoing discussion points to three significant trophic features of the average ocean-caught anchovy larva. These features are:

1. A lack of increase in food particle size proportional to the increase in length for larvae larger than 4 mm (Figure 3b).
2. A steep decline in feeding incidence beginning at 4.5 mm followed by an increase in this value during the second half of the larval period (Figure 8).
3. A decline in relative morphological condition at lengths from at least 10 mm to 17 or 18 mm, followed by an abrupt increase (Figure 9).

Feature 1 must partly reflect the size spectrum of the available plankton. Arthur (1956) and Beers and Stewart (1970) have shown that there are far more food particles of the size taken by the first feeding larvae (50-100 μm) than there are of larger particles suitable for older larvae (i.e., 200 μm). Sardine and jack mackerel larvae, however, are able to secure increasingly larger food particles (Figures 1, 5). When features 1 and 2 are considered together, it would appear that the average oceanic anchovy larva does not sustain its original feeding intensity.

Growth of laboratory-grown anchovy larvae becomes asymptotic at 6 mm long when fed only *Gymnodinium* and at 20 mm when fed only a combination of *Gymnodinium* and rotifers. This was noted by Hunter (in press), who concluded that it is physically impossible for larvae to ingest enough prey in order to grow when the prey are below a certain size. Therefore, the decrease in relative body depth of the ocean-caught anchovy larva (feature 3) could be directly related to the insufficient increase in food particle size (feature 1).

Feeding intensity of clupeoid larvae decreases with malnutrition (Blaxter and Ehrlich 1974; Hunter in press). If the decline in relative body depth does denote a condition of malnutrition, then the decrease in feeding incidence (feature 2) is correlated with this decline, and might be the causative factor. This might also result in larvae spending a longer residence time at these lengths which would introduce a bias in mortality estimates.

It is important to keep in mind that we are considering larvae which have grown in the ocean and have also been caught by plankton nets. This is the reason that the expression "ocean-caught" rather than "ocean-grown" has been used herein. It might be reasoned that the decline in physical condition is a sampling artifact produced by the plankton net catching an increasing percentage of sick or malnourished specimens of the larger larvae as a result of the larger healthy larvae being more capable of dodging the net. The same reasoning could be applied to the decline in feeding incidence. An examination of the physical condition of over 5,000 sardine larvae (Arthur 1956) revealed that there is a higher percentage of larvae in poor shape (e.g., with liver deterioration) taken in day hauls when healthy larvae can avoid the plankton net. Such evidence led Isaacs (1964) to theorize that day-caught sardine and anchovy larvae represent an approximation of the percentage of the population removed by natural mortality. Assuming this sampling bias, however, it then becomes difficult to explain the increase in both relative body depth and feeding incidence of the older larvae taken by the same sampling methods. Burdick (1969), while examining Hawaiian anchovy (*Stolephorus purpureus*) larvae, observed no difference of feeding incidence or physical condition between samples taken concurrently with 1-m net and a plankton purse seine. Assuming the plankton purse seine captures all larvae, sick or well, he concluded that there is no bias produced by only the healthy larvae being able to avoid the 1-m net.

The average ocean-caught anchovy is significantly less robust at its midlarval lengths than its laboratory counterpart, owing presumably to differences in their respective rations. The first feeding (4-day-old) laboratory-reared anchovy larva spends 85% of the daytime in intermittent swimming, 7% in feeding, and 4% at rest (Hunter 1972). Perhaps the undernourished average ocean-caught larva, in response to the usual suboptimal food densities, conserves its dwindling energy resources by increased resting and waiting for prey to appear within its range.

Hjort (1914, 1926) hypothesized that large-scale mortality will result if the proper food is not available in sufficient quantity at the "critical period" when newly hatched fish larvae require their first feeding, and that the numerical strength of a year class, therefore, might be determined at this time. The increasingly thin shape of young ocean-caught anchovy larvae suggests that feeding problems may exist for sometime into the larval period. Saville (1971) proposed that a "critical stage" might occur at any stage between hatching and metamorphosis and that the detection of same would allow one to specify the earliest stage at which reliable indices of year-class strength could be determined. The end of the decline in relative body depth of the average ocean-caught larva might mark the point in the larva's development when the danger of starvation has diminished and perhaps, as suggested by Saville, is the earliest stage at which estimates of recruitment might be made.

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DAILY GROWTH INCREMENTS IN OTOLITHS FROM LARVAL AND ADULT FISHES

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ABSTRACT

Daily growth increments have been found in otoliths of fish larvae. The daily nature of these layers was verified by examining larval fish of known age reared in the laboratory. A simple technique for observing these marks is described and can be used on otoliths from larvae and adults. This provides a convenient method for determining early growth in fishes and is particularly useful for fishes which do not lay down annual or seasonal rings.

The use of otoliths in age determination (by means of annual marks) is well known. The techniques used have been described by Williams and Bedford (1974) and Blacker (1974). Recently Pannella (1971) has suggested that daily marks may be formed in the sagittae (the otoliths used almost universally in age determinations) of some temperate species, while in 1974 Pannella claimed to have detected them in a number of tropical species. He also studied the temperate species—silver hake, *Merluccius bilinearis*; red hake, *Urophycis chuss*; Atlantic cod, *Gadus morhua*; and winter flounder, *Pseudopleuronectes americanus*—in greater detail in this latter paper. For some of these temperate species, particularly for the first, Pannella was able to show that there were fortnightly, monthly, and annual patterns. The annual marks detected in the conventional way were shown to contain about 365 daily units. Pannella used acetate replicas of ground otoliths which had been previously etched with HCl. Pannella's work appears to justify the following conclusions:

1. Daily increments[4] occur in certain temperate fish, e.g., *M. bilinearis*.
2. Periodic variations in increment thickness occur with fortnightly, monthly, and annual frequencies in this species.
3. Structural units that are similar to those shown to be daily in their occurrence in temperate species are also found in some tropical species.

Pannella (1974) was careful to explain that the marks present in otoliths of tropical fish that appeared to be annual on the basis of conventional criteria could be deceptive. He suggested that by analogy with temperate species, certain structures found in otoliths of tropical fish were also daily in occurrence. Although he found spawning marks, he did not find any seasonal or winter growth checks in the otoliths of tropical fish. In view of Pannella's expressed skepticism about the formation of annual marks and his tentative conclusions, further evidence is needed that daily increments occur in tropical fish. Furthermore, no one appears so far to have attempted to apply this method of age determination to larval fish, yet it is in this last area that the most accurate and useful results might be expected. Pannella (1974) commented on the great regularity of the presumably daily marks near the center of the otoliths of both tropical and temperate fish. In these portions of the otoliths, no superposition of more complex patterns (e.g., 14 day, 28 day) were found.

It is the object of this paper to show that 1) true daily increments are found in the otoliths of the larvae of several species, and that daily marks may be used to determine the ages of larval fish with great accuracy and precision, at least for approximately the first 100 days of life; and 2) in adults of fish from a variety of habitats, including tropical waters, daily increments may be proven to exist, and so to confirm Pannella's work.

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[4] The smallest visible concentric layers seen in an otolith.

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METHODS

Some material was examined with a Stereoscan[5] S4 scanning electron microscope (Cambridge Scientific Instruments Ltd.). These otoliths were prepared for viewing by embedding them in polyester resin, grinding and polishing them to the vertical mid-sagittal plane with a graded series of silicon carbide or aluminum oxide compounds (400, 600, and 900 grit), and finishing with 1-μm diamond paste. The polished surface was then etched with 0.1 N HCl before being rotary coated in a vacuum evaporator with 150 Å of gold-palladium alloy.

Both this technique and that of Pannella (1974) involve the use of equipment and materials that may be inaccessible in many countries. This is particularly true for those countries in which daily growth increments might prove to be especially helpful in stock assessment of commercial fish, so that an alternative practical method with minimal equipment was also used here and found to be successful.

Otoliths of adult fish were ground by hand on a glass plate covered with a water-silicon carbide powder mixture (400-600 grit). The final polish may be administered with diamond paste, but this step is not essential. The ground otolith was then examined in immersion oil. The grinding was done in the same plane as described by Pannella (1974). It is possible that storage in oil over a long period of time may reduce the resolution obtained when an otolith is examined. This appears to be particularly true for larval otoliths. The above technique is simple and requires only a good compound microscope. Magnifications used in this work ranged to 1,800×; at least 600× is required for general viewing.

Otoliths from larvae were removed by teasing them from fresh specimens. Oven-dried material needed only to be moistened with a drop of water before otolith removal. The otoliths were manipulated and transferred to clean slides by picking them up on the end of a fine dissecting needle wetted with immersion oil. No additional preparation was necessary, and the otoliths were examined in immersion oil or after being permanently mounted under a cover slip in a quick-drying, neutral mounting medium. Ground sections from juveniles and adults may be similarly mounted with no apparent loss in clarity. Larval otoliths are thin enough that only optical sectioning (i.e., carefully focusing to the plane of maximum clarity) is necessary to make total increment counts.

Material from a variety of species was examined and larval material of known age was obtained by rearing eggs that had been fertilized in the laboratory (Lasker et al. 1970; Leong 1971). The chronological age from these fish was known and could be compared with the number of growth increments observed in their otoliths. Larvae of northern anchovy, *Engraulis mordax*, were kindly made available to us by John R. Hunter of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, at La Jolla, Calif.

RESULTS

Otoliths of 15 *E. mordax*, aged 6 days, were examined. The mean total length of the fish was 4.5 mm. The yolk-sac had been absorbed by the fifth day after hatching. Figure 1a shows the appearance of the otolith of one of these fish.

Only one or two daily increments were present, suggesting that daily growth increments appeared in the otoliths of *E. mordax* only after completion of yolk-sac absorption. In the laboratory, anchovy larvae were maintained in 14 h of light when feeding took place and 10 h of darkness when no feeding occurred (Lasker et al. 1970).

Table 1 shows the relation between chronological age and number of apparently daily increments for larvae of *E. mordax* aged 6 to 100 days. It is clear that there is an extremely close correspondence between the chronological age in days and the number of increments. Figure 1b is a micrograph showing the daily increments in an anchovy otolith from a larva 18 days old.

Additional data presently being collected on laboratory and wild-caught larvae indicates that there is some interaction between the rate of larval growth and the rate of increment formation which may complicate the interpretation of otolith age estimates.

Figure 2 shows the structure of adult anchovy otoliths with successively greater magnification of the scanning electron microscope. The darker areas in the photographs represent areas of the otolith that were more heavily etched because they contained a higher proportion of $CaCO_3$, while the lighter areas have relatively more organic material, probably otolin (see Degens et al. 1969). It is seen from Figure 2 that the smallest

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

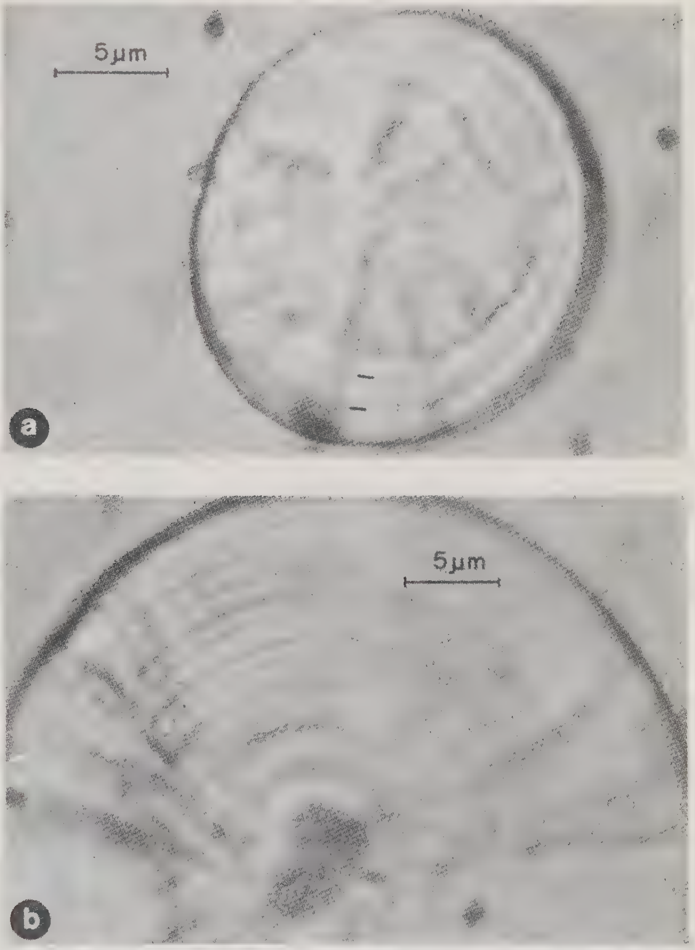

FIGURE 1.—Light microscope photographs of otoliths from laboratory-reared northern anchovy: a) 8-day-old larval otolith showing two daily growth rings; b) 18-day-old larval otolith showing 12 daily growth rings.

TABLE 1.—Chronological age (days from hatching) and numbers of growth increments in otoliths of northern anchovy.

Number of fish	Chronological age in days	Chronological age less 5 days	Mean number of increments	Range
15	6	1	1	0- 2
10	8	3	3	2- 4
10	12	7	7	4- 8
10	15	10	10	8- 11
7	16	11	10	9- 11
5	18	13	13	12- 15
7	20	15	15	14- 16
8	24	19	18	16- 19
9	25	20	20	18- 21
3	26	21	21	18- 23
4	94	89	97	95-100

cyclical units are 1 to 2 µm thick in this part of the anchovy otolith and that they do not appear to contain any smaller units. It is these units that are counted and appear in the data in Table 1. The daily increment would therefore appear to be the smallest unit of growth that is formed at the supra-molecular level and, as such, is in principle the most natural unit to use for age estimation.

Fertilized eggs of the California grunion, *Leuresthes tenuis*, were obtained and reared in the laboratory. The larvae were maintained in a natural light cycle at 17° to 20°C with food (*Artemia* nauplii) continuously available. Larvae were sacrificed at intervals and their otoliths were examined. Table 2 shows the results obtained and Figure 3 shows a photograph of a grunion otolith.

Table 2 shows that there is a close relation between the number of growth increments and the chronological age of the larvae. Although the agreement between age and daily increments is not as good as it is for the anchovy, the results are still very good. Table 2 also shows that in *L. tenuis*, daily increments appear at hatching, rather than at yolk absorption. Prehatching marks also occur, although they were not tallied in Table 2. Clearly the exact timing of the initiation of daily increment formation varies from

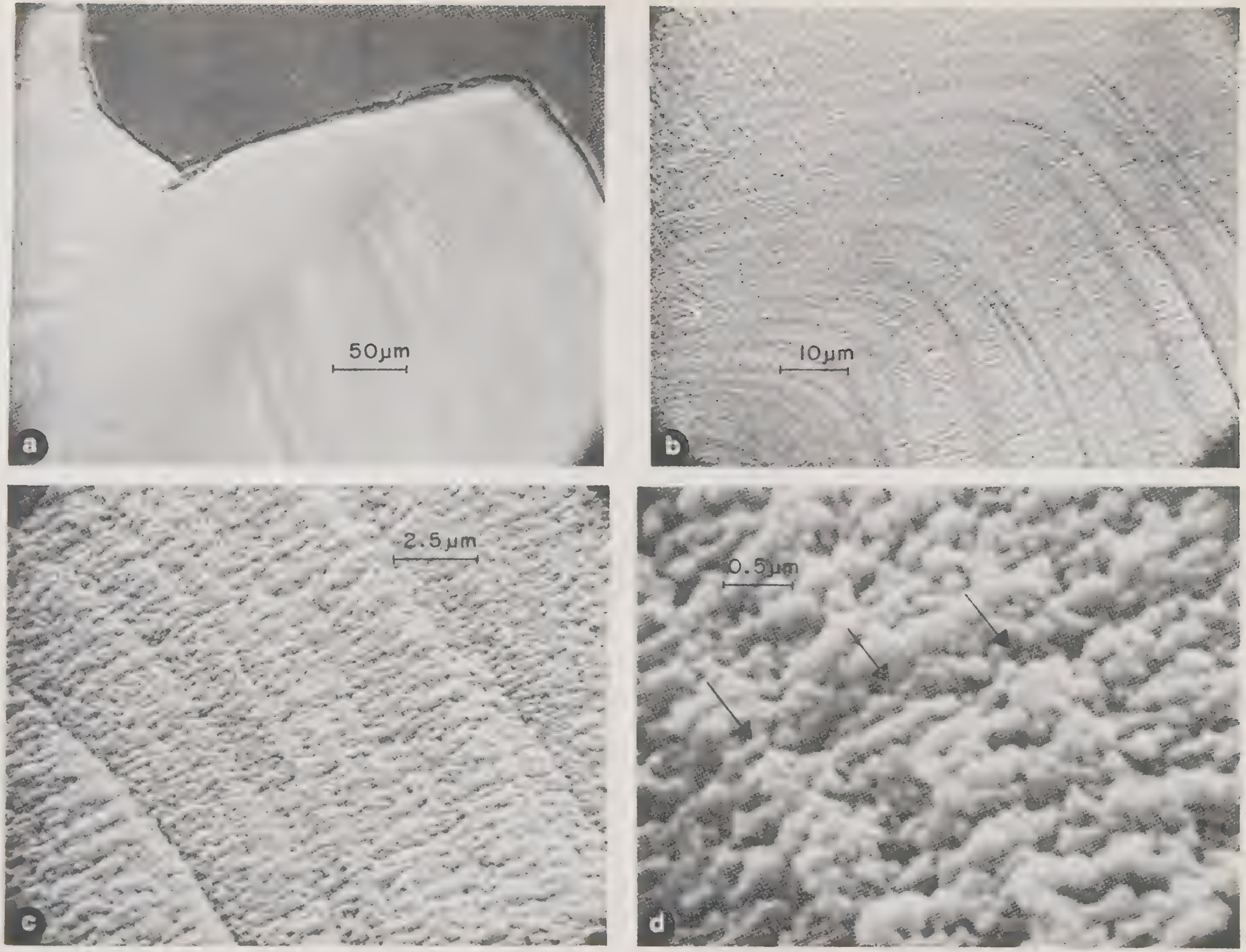

FIGURE 2.—Scanning electron microscope photographs of an otolith from a 2-yr-old northern anchovy Successively higher magnifications are shown in a through d. At highest magnification, the distance between daily marks (indicated by arrows) is shown to be between 1 and 2 μm.

TABLE 2.—Chronological age and number of growth increments in the otoliths of the California grunion.

Number of fish	Chronological age in days	Mean number of increments	Range
2	0	2	1- 2
3	7	9	8-10
2	16	11	10-12
3	18	17	16-18
5	26	24	20-26

species to species and must be independently determined for each one.

Young striped bass, *Morone saxatilis*, were collected on 2 July 1974 in the Sacramento River delta (Tracy Pumping Station), Calif. These five fish measured 29 to 37 mm SL (standard length) and their otoliths had 62 to 120 observable increments; i.e., a sample of striped bass which should have been 2 to 4 mo old according to their known spawning season (Scofield 1931) were 2 to 4 mo old according to the presence of growth layers found in their otoliths. The spread in the age calculated from daily increments probably corresponds to a considerable spread in the dates when the fish examined were hatched.

Otoliths from two striped bass 135 and 142 mm SL were also examined. Published information on the growth rate of this species (Scofield 1931) indicates that striped bass of this size taken in July should be 14 to 16 mo old. The ages obtained by counting the presumed daily growth marks were 419 and 445 days respectively, i.e., 14 to 15 mo old.

Figure 4 shows the daily marks in an otolith of striped bass. Daily increments were fairly thick near the center, thinner in an intermediate area corresponding to the hyaline zone, and wider again near the edge. In one specimen the central

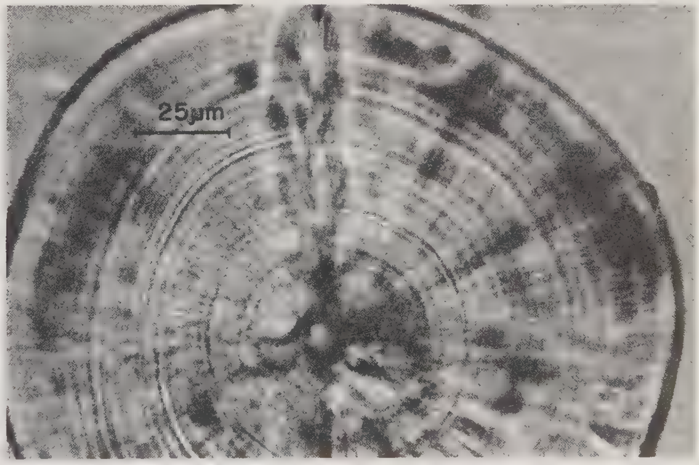

FIGURE 3.—Daily growth rings in an otolith of a California grunion larva. The larva was approximately 26 days old.

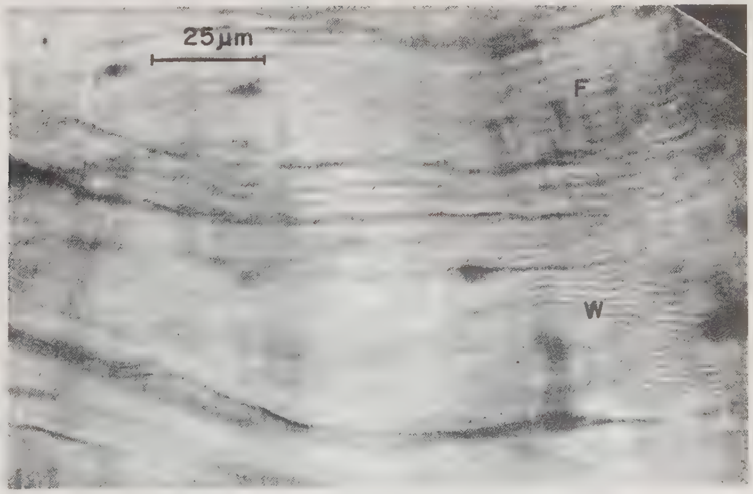

FIGURE 4.—Daily growth rings in a striped bass otolith. This fish was approximately 15 mo old. Differential growth can be seen in rings grown in adjacent seasons. F = fall; W = winter.

area contained 231 daily increments, the marginal area contained 120, and there were 94 thinner marks in the middle zone. Working backwards from the 2 July collection date, this indicated the slow growth zone occurred in December, January, and February. These figures correspond well with the known life cycle (Scofield 1931) which suggests a fast growth period in spring, summer, and fall (230 days, ≈ 8 mo), a short winter of slow growth (≈ 3 mo), and a spring and early summer (≈ 4 mo) of faster growth prior to capture.

Otoliths of postlarvae of the gobies *Clevelandia ios, Ilypnus gilberti*, and *Quietula y-cauda* were also examined. The fish were collected in Mission Bay, San Diego. The 2-mo larval period indicated in the otoliths agree with several independent estimates of the length of time between hatching and settlement (Brothers 1975).

Otoliths of two species of hake obtained from the Gulf of California were studied. Mathews (1975) has shown that annual marks (annuli) may be detected by means of the usual discrimination of hyaline and opaque zones in *Merluccius angustimanus* while in *Merluccius* sp. (Mathews in press) the same techniques have also been applied successfully. The ages of hake determined by means of annuli may be compared with age determined from counting the number of daily increments; these are identified by analogy with the structures shown to be daily in their incidence in anchovy, grunion, striped bass, and other fish and which appear to be the same as those shown by Pannella (1971) to be daily in *M. bilinearis* (Figures 5, 6). In most cases, direct total counts were not possible because increments were not equally visible over a complete nucleus to margin radius. For these otoliths measurements of incre-

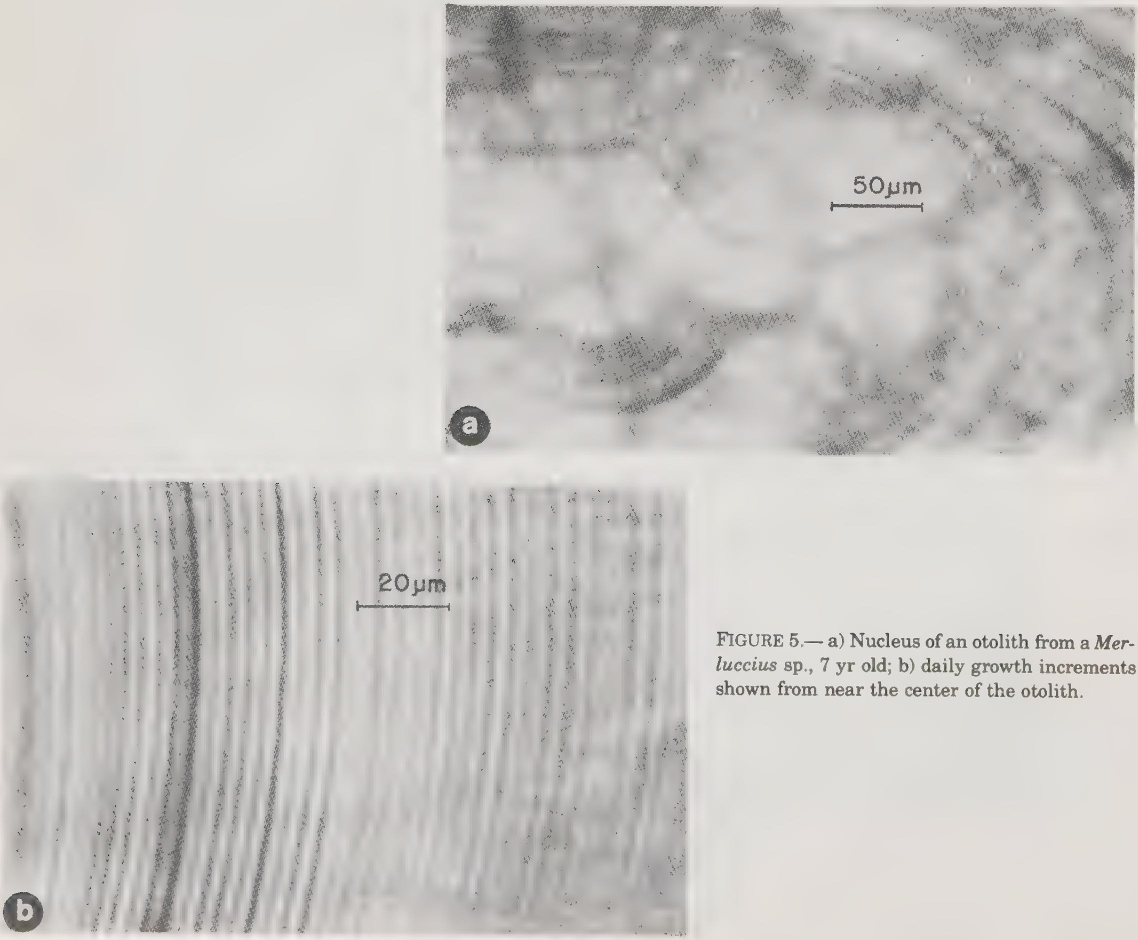

FIGURE 5.— a) Nucleus of an otolith from a *Merluccius* sp., 7 yr old; b) daily growth increments shown from near the center of the otolith.

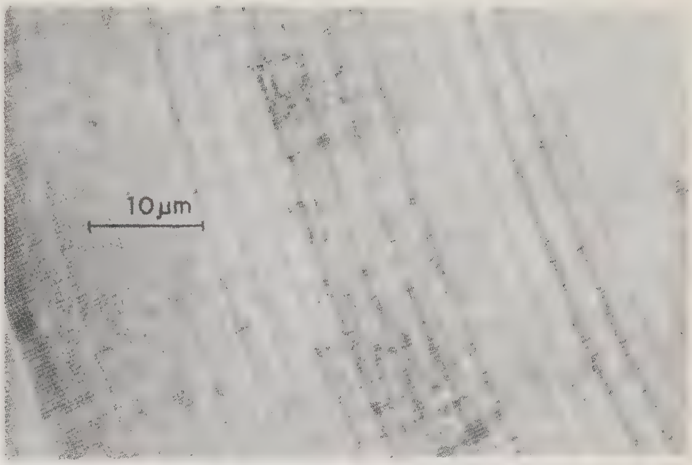

FIGURE 6.—Daily growth increments from the otolith of *Merluccius angustimanus*. Note radial fibers crossing the growth layers.

ment width were made at five or more locations along a radius and then total counts were calculated by extrapolation. No larval or very young hake were available for examination.

For *Merluccius* sp., data were available for 22 specimens aged 1 to 7 yr from the annuli present in their otoliths. Figure 7 shows the graph of age by annuli against age by daily increments for this species. The correlation coefficient was 0.91 (20 df, $P >> 0.001$). The slope of the regression line was 1.14 (99% confidence limits [C.L.], 0.81-1.46). This is not significantly different from the value of 1.00 expected if age by years and by days were to yield identical values.

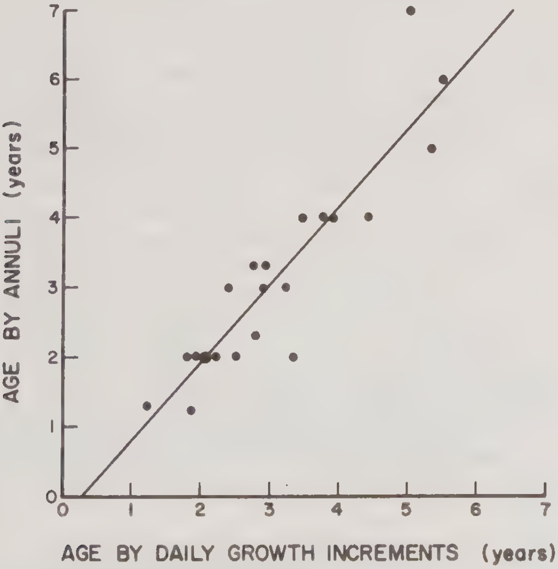

FIGURE 7.—Graph of age-by-annuli against age-by-daily-growth-rings in the otoliths of *Merluccius* sp. The encircled point represents two points at the same position.

Data from seven specimens of *M. angustimanus* were available and they varied in age from only 1 to 2 yr. Given the much narrower ranges and the smaller sample, the results obtained were acceptable: r = 0.74 ($0.05 > P > 0.01$) and the slope of the line was 1.25 (99% C.L., 0.24-2.25); i.e., the slope was significantly different from zero, but not from 1.0.

The precision of estimates of age obtained for *M. angustimanus* was not very good, with deviations of up to 0.5 yr being obtained; however, for *Merluccius* sp. a somewhat narrower range was usual, with some values differing by 0.1 yr or less. Extreme variations occurred with fish aged 7 to 13 yr, where errors of up to 2 to 3 yr could be obtained where daily counts were made.

The average widths of the daily bands found in the hake otoliths were 3 to 4 μm, with wider and narrower bands appearing sometimes in apparently weekly, fortnightly, and monthly units. The incidence of these units has not been examined in detail and requires further study, but preliminary work suggests that the basic unit used in age estimates should be the daily unit; the higher order units may be of great ecological interest, but should probably not be used in aging these hake: Only daily increments occur with the necessary consistency and regularity.

In addition to the species mentioned above, apparently daily marks have been found in a wide variety of other fish, e.g., in *Tilapia zilli*, *T. nilotica*, and *Clarias mossambicus* from Lake Victoria (examined by E. B. B. and C. P. M.; specimens kindly collected by John Rinne and Dr.

Peretti of the East African Freshwater Fisheries Research Organization, Jinja, East Africa), and the following species examined by one of the authors (E.B.B.): in the deep living Pacific rattail *Coryphaenoides acrolepis* (58 cm SL; 10 to 11 yr); in the myctophids *Stenobrachius leucopsarus, Tarletonbeania crenularis,* and *Triphoturus mexicanus*; in the freshwater fish *Cottus asper* and *Salmo gairdneri*; in the tropical marine fish *Chromis atrilobata* and *Apogon retrosella*; in adults of the gobies *Clevelandia ios* and *Gillichthys mirabilis*, where clear growth checks also occur, so that daily marks alone would lead to distinct underestimates of age; and in four species of rapidly growing tropical and temperate tunas. Statoliths from the squid *Loligo opalescens* (both wild caught adults and laboratory-reared juveniles) also show what appear to be growth layers analogous to those in fish otoliths. The appearance of growth interruptions in a number of species, e.g., the rockfish (genus *Sebastes*), either as winter checks, spawning checks, or apparently dispersed more evenly throughout the year, may impose a severe limitation upon the use of daily marks to age these fish. The technique seems best suited to larvae, juveniles, fast-growing species, and tropical species.

It is clear from our work that some difficulties must be overcome before age estimation by means of daily rings can become a standard tool in fisheries biology. However, it is also clear that

1. Daily rings may be used to estimate the ages of larvae of some species up to 100 days old with very great precision and that they probably can be used for fish up to 1 yr of age, perhaps with a smaller degree of precision. Struhsaker and Uchiyama (1976) show similar results with the tropical engraulid *Stolephorus purpureus.*

2. Daily marks may be used as a means of accurate age determination for at least some species of fish up to 6 yr old.

3. Daily marks may be used for age determination of at least some tropical fish. Pannella's (1974) suggestion that daily increments might be used in tropical fish as a means of age estimation is almost certainly true, and should be applicable to most species.

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REVIEW OF THE DEEP-SEA FISH GENUS *SCOPELENGYS* (NEOSCOPELIDAE) WITH A DESCRIPTION OF A NEW SPECIES, *SCOPELENGYS CLARKEI*, FROM THE CENTRAL PACIFIC

John L. Butler[1] and Elbert H. Ahlstrom[2]

ABSTRACT

Scopelengys has been known previously from a few widely scattered collections. Recent collections by the Scripps Institution of Oceanography in the Pacific, the RV *Walther Herwig* in the Atlantic, and the International Indian Ocean Expedition have made possible a critical study of this genus. No significant differences were found in either morphometric characters or meristic counts between specimens of *S. tristis* Alcock from the eastern North Pacific (lat. 16° to 33°N, long. 117° to 126°W) and those from the eastern South Pacific (lat. 5° to 16°S, long. 77° to 90°W). When Pacific Ocean specimens were compared with those from the Atlantic and Indian oceans, no significant differences were found in morphometric characters, and although differences in average meristic counts were somewhat larger between oceans than among Pacific specimens, such differences exceed one for only one meristic character (gill rakers), and the ranges for all counts from all oceans almost completely overlapped.

Scopelengys clarkei is described from the central North Pacific. It differs from *S. tristis* mainly in pectoral ray count (2.5 average difference), average counts of vertebrae (3.3 average difference), deeper caudal peduncle, narrower maxillary, and in a differently pigmented larva.

In 1890, Alcock described a new genus and species, *Scopelengys tristis,* from a single denuded specimen collected in the Arabian Sea. Although there was no evidence of photophores, Alcock placed his new genus in the family Scopelidae (=Myctophidae) allowing that the "exact position among the Scopelidae cannot be accurately defined at present." Garman (1899) described *S. dispar* from two specimens collected in the Gulf of Panama. Garman distinguished *S. dispar* from *S. tristis* by its lower dorsal- and anal-fin ray counts. *Scopelengys dispar* was considered a junior synonym by Parr (1928), Bolin (1939), and Norman (1939). Until 1963, *Scopelengys* was known only from the Indian and Pacific oceans. Its discovery in the Caribbean Sea by Mead (1963) resulted in the description of a third species, *S. whoi* Mead.

A recent survey of mid-water fishes conducted by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) provided us with specimens which indicated that two species of *Scopelengys* were present in the Pacific Ocean. Additional specimens made available to us by Thomas A. Clarke of the Hawaiian Institute of Marine Biology (see in this regard Clarke 1973), confirmed that the second form was an undescribed species. Study of *Scopelengys* from the Atlantic, Pacific, and Indian oceans indicates that *S. dispar* and *S. whoi* Mead are synonyms of *S. tristis* Alcock.

METHODS AND MATERIALS

Measurements were made following Hubbs and Lagler (1958). Measurements are given in percent of standard length (SL), unless indicated otherwise. Only lath-shaped gill rakers on the first gill arch are included in gill raker counts. Vertebral counts were determined from radiographs; the urostyle was included as one vertebra.

Morphometric and meristic data were obtained from 211 specimens from the Atlantic, Pacific, and Indian oceans. Subsamples equal to the smallest *N* (32 in the Atlantic) were randomly taken from the Indian Ocean, the eastern North Pacific between lat. 16° and 33°N and long. 117° to 126°W, and the eastern tropical Pacific between lat. 5° and 16°S and long. 77° to 90°W. Morphometric data were compared by analysis of covariance. Meristic data were compared by Tukey's multiple comparison procedure at the 5% level (Rothschild 1963).

Material was examined from the following collections: Scripps Institution of Oceanography

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(SIO); University of Southern California (USC); Institut für Seefischerei, Hamburg (ISH); Museum of Comparative Zoology (MCZ); U.S. National Museum (USNM); International Indian Ocean Expedition (IIOE); and Field Museum of Natural History (FMNH).

GENUS *SCOPELENGYS* ALCOCK 1890

Type-species *Scopelengys tristis* Alcock, by monotypy.

Description.—Head and body laterally compressed, eyes small, mouth large. Premaxillary, dentary, and palatines with bands of villiform teeth. Teeth absent at symphysis of upper and lower jaw. Vomer indented at head with teeth in two patches. Teeth on basihyal and on gill rakers. Anterior gill rakers reduced to toothed knobs. Maxillary extending past eye, expanded posteriorly. Supramaxillary present. Head and body covered with large deciduous, cycloid scales. Pectoral fins lateral, extending beyond bases of pelvic fins. Pelvic fins abdominal. Origin of dorsal fin about over base of pelvic fin. Anal fin completely behind dorsal. Base of adipose fin over posterior half of anal fin. No photophores. No swim bladder in adults.

D 11-13; A 12-14; P 12-17; V 8; Br 8; C principal 19 (1 + 17 + 1); procurrent C 6-9 dorsal and 7-8 ventral, hypurals (including parhypural) 4 + 3; epurals 3; uroneurals 2. Urostyle with two centra. As in all myctophiform fishes retaining two ural centra (personal observation reenforced by Rosen and Patterson 1969), the anterior ural centrum (labelled $PU_1 + U_1$ in Rosen and Patterson) supports both the parhypural and the 2 inferior hypurals, whereas the posterior ural centrum (U_2 in Rosen and Patterson) is associated exclusively with the 4 superior hypurals.

Scopelengys tristis Alcock

Scopelengys tristis Alcock 1890:302.
Scopelengys dispar Garman 1899:254, plate 54, fig. 2-2d.
Scopelengys lugubris Garman 1899:400, (synonym *Scopelengys dispar).*
Scopelengys whoi Mead 1963:255, fig. 1.

Description of Adult

Body moderately slender, maximum body depth at nape, tapering to a narrow caudal peduncle (Figures 1A, 2A); body depth at dorsal origin 11.7-19.8 (15.4); least depth at caudal peduncle 5.6-8.3 (6.8). Dorsal profile of head slightly concave; head length 24.4-33.9 (29.4); head depth 16.7-25.5 (20.2); eye small, orbit 3.1-4.2 (3.5); snout 7.5-10.1 (8.8). Width of maxillary as percentage of its length 29.9-36.7 (32.2). Snout to: dorsal fin origin 36.1-47.0 (41.9); anal fin origin 56.4-72.6 (66.4); ventral fin origin 34.7-48.0 (41.8).

Meristic Data.—D.11-13 (11.5); A 12-14 (13.0); P 14-17 (15.4); vertebrae 29-32 (30.8); total gill rakers 7-11 (8.5).

Larvae

Twenty-five specimens 3.5-10.3 mm were available from the eastern Pacific. Measurements and counts were given for two eastern Pacific (EASTROPAC) specimens (6.2 and 6.4 mm SL) by Okiyama (1974) and the smaller specimen illustrated. The larvae have a small round eye without choroid tissue, a snout as long proportionately as in adults, a gut terminating just forward of the anal fin, and a gas bladder, best seen on late preflection and flexion specimens, becoming obscured by overlying musculature in larger postflexion specimens.

Rays form early in the pectoral fins; a 3.5-mm specimen has large pectorals extending posteriad to the anus; caudal fin forms and notochord flexion occurs between ca. 5 and 7 mm; dorsal and anal fins form during flexion; pelvic buds appear between 6.5 and 7.0 mm; fin formation, including procurrent caudal rays, complete by about 10.0 mm. Pigmentation is scanty; pigment develops on dorsal margin of peritoneal cavity, spreading laterally on preflexion and flexion stage specimens but becoming obscured on postflexion larvae; preflexion larvae have a series of 6 or 7 small, inconspicuous spots along the ventral margin of the tail which are later obscured by the anal fin formation and lacking on late postflexion larvae; head pigment, best developed on postflexion specimens, consists of a striking horizontal bar extending from snout to eye and continuing behind the eye onto the operculum (Figure 3A).

Distribution

Records are from the tropical Atlantic, Pacific, and Indian oceans (Figure 4). The range is expanded poleward in the eastern part of the Pacific

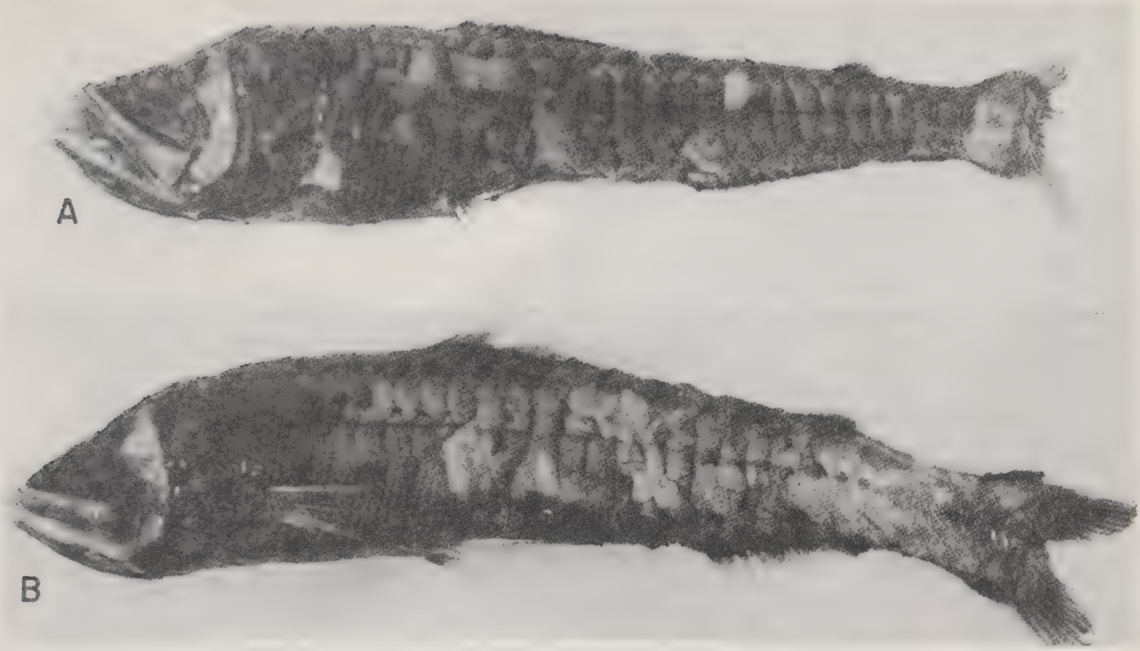

FIGURE 1.—A: *Scopelengys tristis*, 126 mm, *Velero IV*, cruise 1238, stn. 18762/10. B: *S. clarkei*, 176 mm. SIO 73-160, holotype.

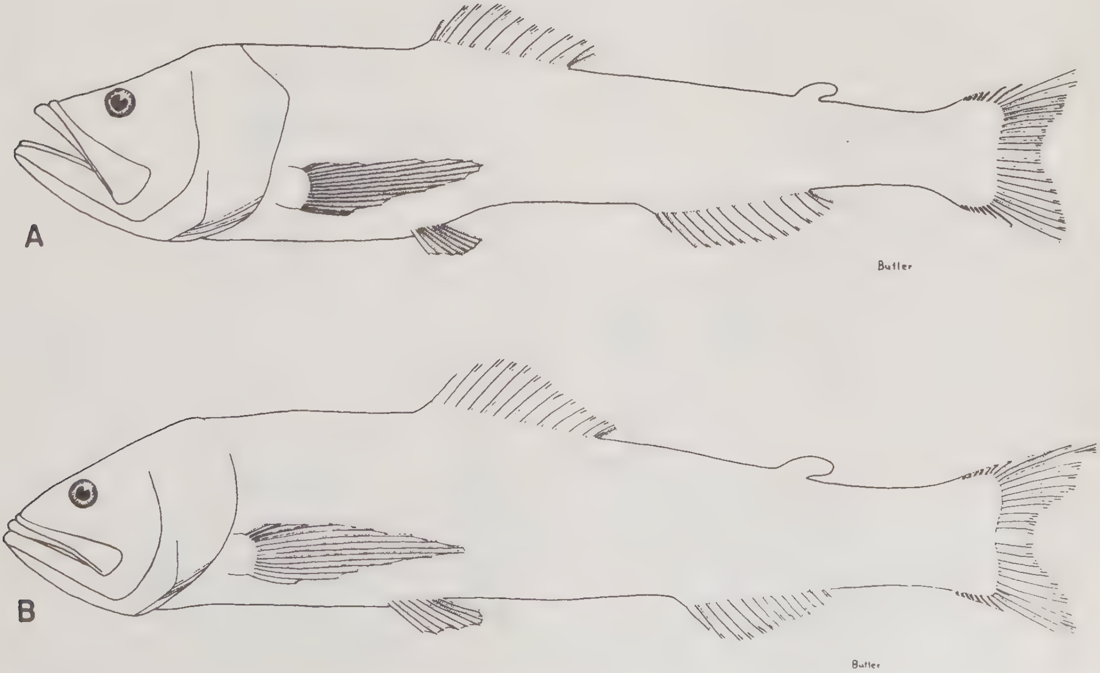

FIGURE 2.—A: *Scopelengys tristis*, 126 mm, *Velero IV*, cruise 1238, stn. 18762/10. B: *S. clarkei*, 176 mm. SIO 73-160, holotype.

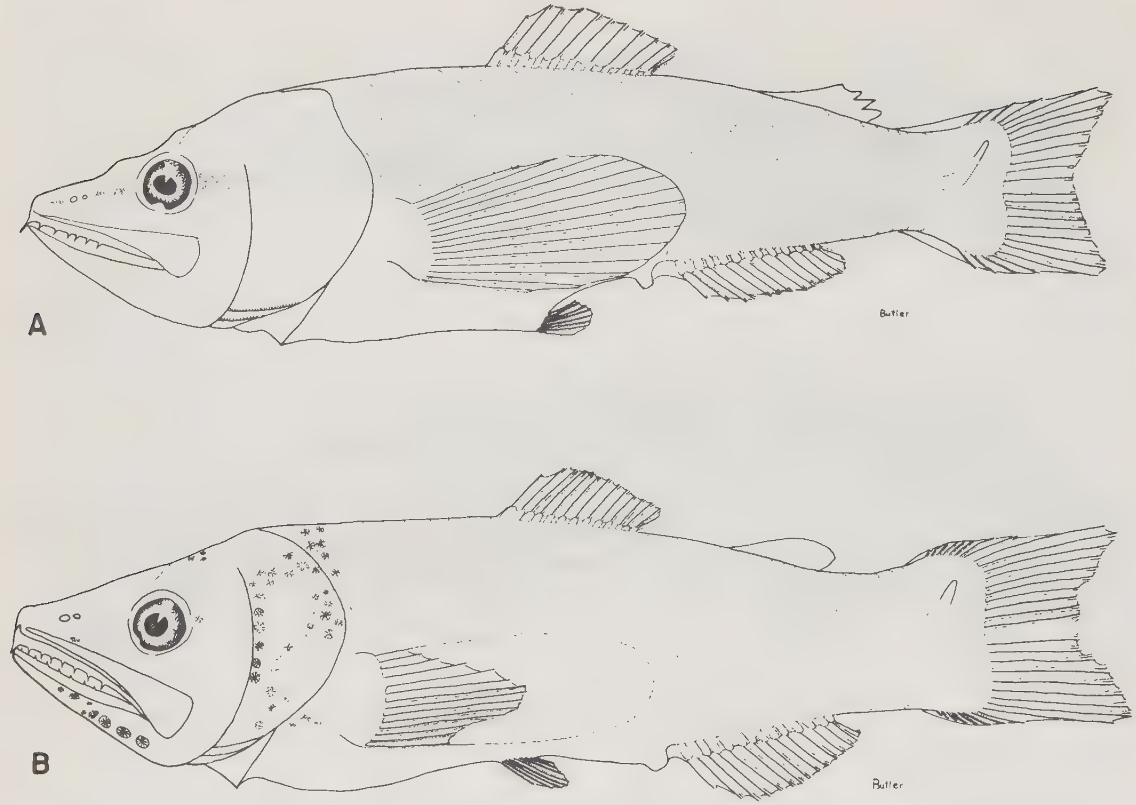
A
Butler
B
Butler

FIGURE 3.—A: *Scopelengys tristis*, 13.9 mm, from the western Indian Ocean. B: *S. clarkei*, 15.4 mm, from off Hawaii.

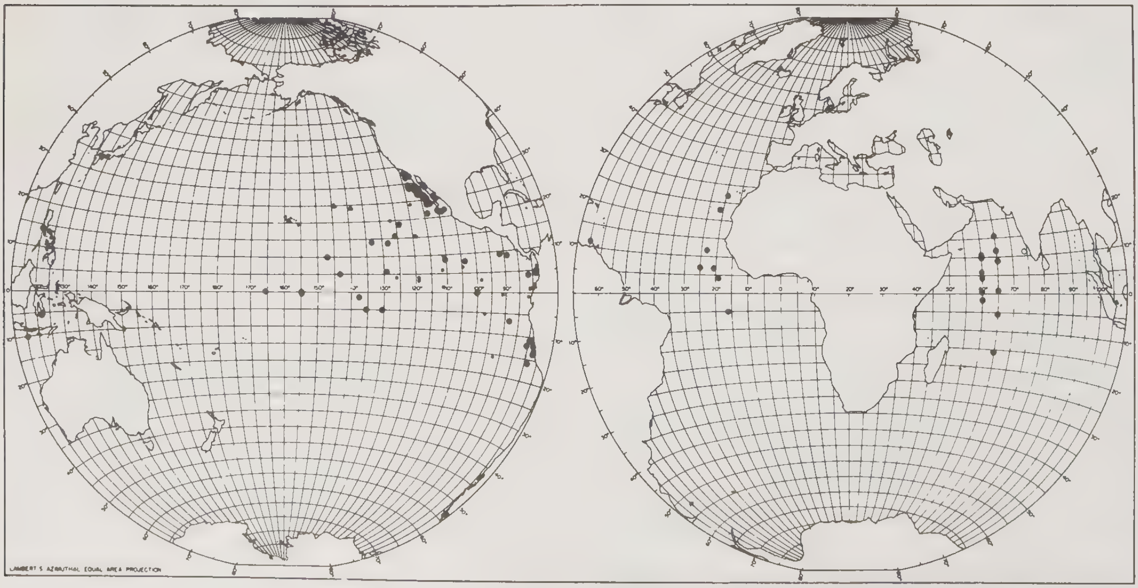
LAMBERT'S AZIMUTHAL EQUAL AREA PROJECTION

FIGURE 4.—Distribution of *Scopelengys tristis* (circles) and *S. clarkei* (triangles). Small symbols indicate larvae.

and Atlantic oceans and is narrowed along the equator to the west. In the western part of the Pacific and Atlantic, the species appears to be rare. Records of larvae from the Indian Ocean were presented by Nellen (1973).

Geographic Variation

Most of the specimens studied from each area were in poor condition, which added to the variability of body proportions (Table 1). No significant difference was found in any morphometric character between regions. Meristic characters of 32 specimens each from four areas are presented in Table 2. Samples from the two eastern Pacific areas showed no significant differences between means of any meristic character. Indian Ocean specimens differed from Pacific material in mean vertebral counts (30.4 vs. 30.9), pectoral-fin ray counts (15.2 vs. 15.7), and in gill raker counts (9.1 vs. 7.9). Atlantic material differed from Pacific material in dorsal-fin ray counts (12.0 vs. 11.4), in anal-fin ray counts (13.4 vs. 12.8), in gill raker counts (9.2 vs. 7.9), and in pectoral-fin ray counts (15.0 vs. 15.7). Atlantic material differed from Indian Ocean material in dorsal-fin ray counts (12.0 vs. 11.1), anal-fin ray counts (13.4 vs. 12.9), and vertebral counts (31.1 vs. 30.4). Although these differences are small, they are as marked between Indian and Atlantic ocean specimens as be-

TABLE 1.—Comparison of morphometric characters of *Scopelengys tristis* from four geographic areas (*N* = 32 for each area).

	Eastern North Pacific		Eastern tropical Pacific		Indian Ocean		Atlantic Ocean	
Character	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Standard length (mm)	124.0	73.8-154.3	130.2	74.5-172.0	104.6	28.8-185.9	133.1	69.5-185.8
Head length	30.9	28.7- 33.9	28.5	28.2- 33.2	30.5	27.8- 33.5	27.6	24.4- 32.2
Head depth	20.2	18.6- 25.5	20.0	16.7- 22.5	20.9	17.2- 24.6	19.6	17.5- 21.7
Snout to origin of dorsal fin	42.7	39.6- 45.5	42.5	39.5- 46.2	41.9	36.1- 47.0	40.6	37.1- 43.6
Snout to origin of pelvic fin	41.7	39.4- 45.3	42.8	39.4- 48.0	41.2	34.7- 46.1	41.6	37.8- 46.9
Snout to origin of anal fin	66.3	63.0- 69.5	67.5	62.5- 72.1	65.2	56.4- 71.2	66.6	61.3- 72.6
Least depth of caudal peduncle	6.8	5.7- 8.1	7.0	6.1- 7.9	6.7	5.6- 8.3	6.9	5.9- 8.0
Body depth at origin of dorsal fin	16.0	13.3- 19.4	15.6	12.6- 19.3	14.5	11.7- 17.2	15.7	12.6- 19.8

TABLE 2.—Meristic data for *Scopelengys tristis* from the eastern North Pacific, eastern tropical Pacific, the Indian Ocean, and the Atlantic Ocean.

Meristic character Area	Numbers of character and frequency					*N*	Mean	Overall mean
Dorsal rays	10	11	12	13				
Eastern North Pacific		18	14			32	11.44	
Eastern tropical Pacific		21	11			32	11.34	
Indian Ocean		28	4			32	11.12	
Atlantic Ocean		2	29	1		32	11.97	11.47
Anal rays	11	12	13	14				
Eastern North Pacific		10	20	2		32	12.75	
Eastern tropical Pacific		8	22	2		32	12.81	
Indian Ocean		5	24	3		32	12.94	
Atlantic Ocean			19	13		32	13.41	12.98
Pectoral rays	14	15	16	17				
Eastern North Pacific		33	24	7		64	15.59	
Eastern tropical Pacific		20	32	12		64	15.88	
Indian Ocean	2	48	14			64	15.19	
Atlantic Ocean		62	2			64	15.03	15.42
Vertebrae	29	30	31	32				
Eastern North Pacific		5	28			32	30.88	
Eastern tropical Pacific		3	25	4		32	31.03	
Indian Ocean	1	20	9	2		32	30.38	
Atlantic Ocean	1	3	21	7		32	31.06	30.84
Gill rakers	7	8	9	10	11			
Eastern North Pacific	10	52	1			63	7.86	
Eastern tropical Pacific	17	39	4	3		63	7.89	
Indian Ocean	1	4	49	7	2	63	9.08	
Atlantic Ocean		2	47	12	2	63	9.22	8.51

tween specimens from these areas and from the Pacific. Because there is no clinal pattern in the variation and because of extensive overlap in all counts, no taxonomic importance was placed on the small meristic differences.

Garman distinguished *S. dispar* from *S. tristis* by the lower dorsal and anal-fin ray counts: D 11 vs. 12 and A 12-11 vs. 13 (Garman 1899). The types of *S. dispar* are in poor condition but the anal fins appear to have 12 or 13 rays (Robert Schoknecht pers. commun.). The counts of *S. dispar* are within the range of *S. tristis*. *Scopelengys dispar* has been correctly considered a junior synonym by Parr (1928), Bolin (1939), and Norman (1939). *Scopelengys lugubris* Garman 1899:400, the specific name regarded as a *lapsus calami* by Bolin (1939), is a synonym of *S. dispar,* hence of *S. tristis*. *Scopelengys whoi* was described from the Carribbean Sea (Mead 1963). The diagnosis was based on a shorter head, higher number of anal fin rays (14 vs. 12-13), and the insertion of the pelvic fin in advance of the origin of the dorsal. According to Mead (1963), however, the head length is ". . .a poor measurement because of the condition of the opercular flap." The anal-fin ray count is within the range of *S. tristis* (Table 3). The insertion of the pelvic fin is a variable character in *S. tristis*. In most specimens the fin is inserted below the origin of the dorsal fin but insertion in advance of the dorsal is not uncommon. Based on this study, we conclude that *S. whoi* is a junior synonym of *S. tristis*.

Study Material

PACIFIC OCEAN ADULTS.—SIO 51-186 1 (134); SIO 64-21 6(78-148); SIO 65-243 2(122-134); SIO 64-997 1(122); SIO 65-244 1(75); SIO 55-229 9(31-113); SIO 65-206 1(92); SIO 60-212 4(20-133); SIO 52-309 2(36-56); SIO 73-170 1(49); SIO 73-171 1(30); SIO 55-265 1(54); SIO 65-620 1(139); SIO 65-606 4(92-151); SIO 65-220 5(14-138); SIO 65-611 17(85-176); SIO 51-84 3(74-123); SIO 69-497 6(92-170); SIO 72-186 8(73-179); SIO 65-215 1(121); SIO 54-124 1(147); SIO 52-367 1(145); SIO 60-232 1(168); SIO 65-213 3(88-158); SIO 60-219 2(42-170); SIO 55-246 4(65-140); SIO 68-579 1(140); SIO 53-235 1(154); SIO 51-146 3(127-144); SIO 65-603 17(62-160); SIO 55-244 2(159-167); SIO 72-195 17(88-175); SIO 65-608 14(43-200); SIO 72-193 2(106-169); SIO 72-192 18(10.2-177); SIO 60-216 2(42-76); SIO 60-218 1(48); SIO 66-355 1(135); SIO 69-19 1(24); SIO 72-182 1(90); SIO 66-407 1(42); SIO 64-24 1(116); SIO 60-234 1(69); SIO 64-13 1(113); SIO 52-409 1(65); SIO 59-202 1(83); SIO 52-90 1(113); SIO 64-15 1(85); SIO 63-444 1(103); SIO 60-243 4(18-44); SIO 68-534 1(28); SIO 65-443 1(142); SIO 68-104 1(97); SIO 60-209 1(78); SIO 52-363 2(56-115); SIO 64-28 3(95-144); SIO 57-43 1(126); SIO 65-237 1(128); SIO 61-32 2(105-106); SIO 63-42 1(109); SIO 66-30 1(113); SIO 51-45 1(132); SIO 60-215 7(19-94); SIO 52-32 1(150); SIO 50-270 2(110-115); SIO 51-77 1(110); SIO 51-189 1(120); SIO 54-82 1(107); SIO 54-102 2(116-147); USC *Velero IV*, cruise 1238, stn. 18762/10; MCZ 41695 2(121-141); USNM 135842 1 (X-ray); MCZ 28058 1 (X-ray) (lectotype *S. dispar* Garman).

PACIFIC OCEAN LARVAE[3].—Larvae taken at 17 EASTROPAC stations and 2 CalCOFI stations as follows: EASTROPAC stations 11.282 1(4.8); 13.105 1(5.5); 13.172 2(6.4, 6.8); 20.018 1(5.5); 30.114 2(4.0, 4.5); 45.032 1(8.1); 45.073 1(6.0); 45.078 1(10.3); 45.293 1(6.6); 45.316 1(6.9); 46.034 1(6.2); 46.096 2(6.7, 6.9); 47.001 1(5.2); 47.005 4(3.5-4.3); 47.035 1(7.0); 47.040 1(5.3); 47.065 1(9.2); CalCOFI 7205-20.127 1(5.0); 4907-112 1(9.1).

ATLANTIC OCEAN.—MCZ 41638 1(X-ray)

TABLE 3.—Means and differences among means of meristic counts of *Scopelengys tristis* from four areas (eastern North Pacific, ENP; eastern tropical Pacific, ETP; Indian Ocean, IO; and Atlantic Ocean, AO) and *S. clarkei*.

	S. tristis									Difference in counts between *S. clarkei* and *S. tristis*	
			Mean					*S. clarkei*			
Meristic character	Range	Overall mean	ENP	ETP	IO	AO	Greatest differences among regions	Range	Mean	Average difference	Least difference
Dorsal rays	11-13	11.47	11.4	11.3	11.1	12.0	0.9	13	13.0	1.5	1.0-AO
Anal rays	12-14	12.98	12.8	12.8	12.9	13.4	0.6	14	14.0	1.0	0.6-AO
Pectoral rays	14-17	15.42	15.6	15.9	15.2	15.0	0.9	12-13	12.9	2.5	2.1-AO
Vertebrae	29-32	30.84	30.9	31.0	30.4	31.1	0.7	34-35	34.1	3.3	3.0-AO
Gill raker	7-11	8.51	7.9	7.9	9.1	9.2	1.3	7-10	8.2	0.3	0.3-EP

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[3] Station data in EASTROPAC Information Paper 6 and Ahlstrom (1972).

(type *S. whoi* Mead); USNM 20678, 5(152-164), eastern tropical Atlantic, lat. 07°32′N, long. 20°54′W, 1813-2125, 12 April 1971, 1,300 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 623/68, 7(73-162), eastern tropical Atlantic, lat. 12°07′N, long. 23°08′W, 30 January 1968, 2,000 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2095/71, 1(167), eastern tropical Atlantic, lat. 05°30′S, long. 16°28′W, 9 April 1971, 1,950 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2447/71, 12(86-160), eastern tropical Atlantic, lat. 04°38′N, long. 19°21′W, 13 April 1971, 756 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 3099/71, 5(132-160), eastern tropical Atlantic, lat. 07°32′N, long. 20°54′W, 14 April 1971, 1,300 m, 1,600-mesh Engels trawl, RV *Walther Herwig;* ISH 2942/71, 2(134-155), eastern tropical Atlantic, lat. 23°47′N, long. 20°59′W, 19 April 1971, 2,100 m, 1,600-mesh Engels trawl, RV *Walther Herwig.*

INDIAN OCEAN[4].—IIOE 7001 *Anton Bruun* III, 16 (25-94); IIOE 7004 *Anton Bruun* III, 7 (32-120); IIOE 7012 *Anton Bruun* III, 2 (23-25); IIOE 7022 *Anton Bruun* III, 1 (113); IIOE 7027 *Anton Bruun* III, 1 (138); IIOE 7037 *Anton Bruun* III, 2 (40-87); IIOE 7046 *Anton Bruun* III, 3 (66-179); IIOE 7143 *Anton Bruun* VI, 1 (131); IIOE 7147 *Anton Bruun* VI, 28 (28-142); IIOE 7153 *Anton Bruun* VI, 4 (42-161); IIOE 7154 *Anton Bruun* VI, 12 (48-114); IIOE 7163 *Anton Bruun* VI, 12 (28-152); IIOE 7165 *Anton Bruun* VI, 3 (22-27); IIOE 7206 *Anton Bruun* VI, 1 (27); IIOE 7277 *Anton Bruun* VI, 2 (40-87).

Scopelengys clarkei n.sp.

Holotype

SIO 73-160, female (176 mm), central Pacific, lat. 29°56.0′N, long. 144°56.6′W, 0224-0556 h; 14 February 1973, 10-foot IKMT, 0-1,000 m, RV *Alexander Agassiz.*

Paratypes

USNM 210707, male (160 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 1204-1637 h; 15 September 1970, 10-foot IKMT, 0-1,000 m, RV *El Pescadero I*; USNM 210706, male (156 mm), central Pacific, lat. 24°N, long. 139°W, 0049-0149 h; 29 November 1972, 50-foot Universal trawl, 0-494 m, RV *David Starr Jordan;* FMNH 76366, female (154 mm), central Pacific, lat. 22°N, long. 158°W, 1240-1645 h; 13 November 1969, 10-foot IKMT, 0-800 m.

Other Materials Studied

SIO 51-76, female (109 mm), southeast of Guadalupe Island, 17 March 1951, 10-foot IKMT, 0-549 m; FMNH 76367, juvenile (65 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 0421-0600 h; 27 February 1971, ⅔ Cobb trawl, 0-150 m, RV *Townsend Cromwell;* FMNH 76368, juvenile (42 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 2236-0105 h; 16-17 November 1969, 10-foot IKMT, 0-250 m, RV *Teritu*; T. Clarke, 71-3-9, larva (15 mm), central Pacific, lat. 21°20-30′N, long. 158°20-30′W, 1252-1645 h; 2 March 1971, 10-foot IKMT, 800-900 m, RV *El Pescadero I,* retained at the Southwest Fisheries Center.

Adult Morphology

Body proportions of the holotype are given first, followed, in parentheses, by range of values for holotype and three paratypes. Body slender; greatest body depth at origin of dorsal fin, 19.0 (18.4-19.0), tapering to a moderately deep caudal peduncle (Figures 1B, 2B), less than three in length of head, 9.4 (9.4-10.2). Head slightly concave in dorsal profile, head length 25.4 (24.5-26.4); head depth 17.6 (16.7-17.9); eye small, orbit 3.0 (2.9-3.6); interorbital width 8.7 (7.6-8.7); snout about one-third of head length, 8.3 (7.7-8.8); length of maxillary 11.3 (11.3-12.6), greatest width of maxillary 3.1 (2.8-3.6). Snout to: dorsal fin origin 43.5 (39.0-43.5); anal fin origin 68.6 (65.1-69.6); pelvic fin origin 40.2 (40.2-43.4). Length of dorsal fin base 17.3 (17.0-19.4); length of anal fin base 16.0 (16.0-17.9). Color dark brown, preserved in alcohol.

Meristic Data

Counts are based on all seven specimens. D 13 (7); A 14 (6), ? (1); P 13/13 (6), 13/12 (1); V 8/8 (7); principal C 10 + 9 (7), procurrent C 7-8/6-9; branchiostegal rays 8/8 (7); vertebrae 15 + 19 = 34 (6), 15 + 20 = 35 (1); gill rakers 1-2 + (6-8) = 7-10 (mean 8.2).

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[4] Station data in Nafpaktitis and Nafpaktitis (1969).

Larvae

A single specimen was available, 15.4 mm SL (Figure 3B). Body shape similar to that of adults but with a relatively larger head—length 35.7 and depth 25.0; eye 5.5; snout 12.8; body depth 23.5; least depth of caudal peduncle, 14.6. Fin origins farther back on body than in adults. Snout to: dorsal fin origin 50.0; anal fin origin 72.8; pelvic base 53.6. Pigment confined to head and nape, extensively developed on the operculum and lower jaw; a small pigment patch on upper jaw behind eye; several melanophores on mid-brain; body pigment confined to nape and to a patch anterior to pectoral base.

Name

This species from the central North Pacific is named in honor of Dr. Thomas A. Clarke of the Hawaii Institute of Marine Biology.

COMPARISON OF *SCOPELENGYS CLARKEI* AND *SCOPELENGYS TRISTIS*

Scopelengys clarkei differs from *S. tristis* in meristic counts, in some morphometric characters, and in larval pigmentation.

For differences in meristic characters, refer to Table 3. Most marked differences are in average number of vertebrae—34.1 (*S. clarkei*) vs. 30.8 =3.3; average pectoral-fin ray count—12.9 (*S. clarkei*) vs. 15.4 =2.5; and average dorsal-fin ray count—13.0 vs. 11.5 =1.5. As regards morphometric characters, *S. clarkei* has a deeper caudal peduncle, a narrower maxillary, and a more fusiform body. Several distinctive adult characters also can be recognized in larger larvae of the two species, i.e., differences in meristic characters and depth of caudal peduncle. The most striking differences between larvae of the two species are found in the head pigment which is restricted to an eye-bar in *S. tristis,* as compared with the scattered pigment on the operculum, lower jaw, etc. of *S. clarkei.*

The two species are similar in general body shape, head size, eye size, length of snout, and position of fins on the body. *Scopelengys clarkei* has its greatest body depth at the dorsal origin, whereas *S. tristis* has its greatest body depth at the nape.

When an analysis of covariance was performed on the morphometric characters of 7 *S. clarkei* and 32 *S. tristis* from the eastern North Pacific, eastern tropical Pacific, Indian, and Atlantic oceans, only the least depth of caudal peduncle

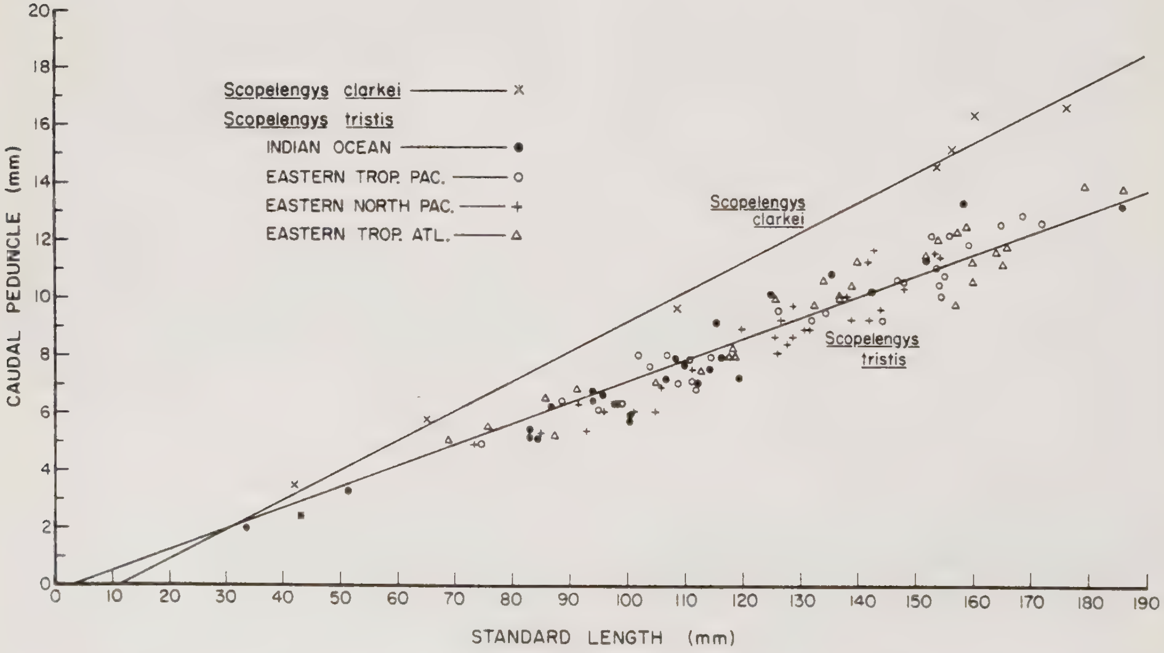

FIGURE 5.—Regression of least depth of caudal peduncle on standard length of *Scopelengys tristis* and *S. clarkei.*

showed a significant difference at the 1% level, $F = 3.72$, between the two species.

The Atlantic specimens of *S. tristis* had counts for four characters that were closer to those of *S. clarkei* than were counts of these characters from other geographic areas. These differences in counts between Atlantic *S. tristis* and *S. clarkei* were as follows: dorsal fin rays 1.0 (12.0 vs. 13.0), anal fin rays 0.6 (13.4 vs. 14.0), pectoral fin rays 2.1 (15.0 vs. 12.9), and vertebrae 3.1 (31.1 vs. 34.2). Differences of two in pectoral-fin ray counts and three for vertebrae are much greater than the regional variability found among specimens of *S. tristis*.

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SHORT COMMUNICATION

PERCEPTION OF ABRUPT TEMPERATURE DECREASE BY RESTRAINED SKIPJACK TUNA, *KATSUWONUS PELAMIS*

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Abstract—1. Decreasing temperature stimuli produced responses and threshold similar to those produced by increasing temperature stimuli in a previous study with skipjack tuna, *Katsuwonus pelamis*.

2. Restrained skipjack tuna signaled by deceleration of heart rate that they could perceive abrupt temperature decreases (0·5°C/sec) as small as 1–2°C.

3. Temperature stimulation of the oral–branchial cavity was more effective in eliciting responses than stimulation of the dorsal, anterior quadrant of the body surface.

INTRODUCTION

Perception of temperature increases by skipjack tuna, *Katsuwonus pelamis*, determined by classical cardiac conditioning was not acute, *ca.* 1–2°C (Dizon *et al.*, 1974). In addition stimuli directed into the oral–branchial cavity were more effective in eliciting responses than stimuli directed onto the dorsal, anterior quadrant of the body surface based on analyzable data from only nine fish.

Our present experiment tests whether skipjack tuna are more sensitive to a decrease in temperature than they were to an increase, and provides additional data on the sensitivity of the skin on the back versus the oral–branchial cavity.

MATERIALS AND METHODS

Thirty-five skipjack tuna (average weight 1·4 kg) were tested for heart-rate decelerations in response to temperature decreases. The technique of cardiac-deceleration testing has been described in detail by Dizon *et al.* (1974).

Briefly, tuna were removed from the holding tanks, secured in a test apparatus with Velcro‡ and immobilized with a muscle relaxant (gallamine triethiodide, 1 mg/kg). Each fish was subjected to two streams of water (8 l/min): one in the oral–branchial cavity (mouth) and one directed at the dorsal anterior quadrant of the body (back). We trained the fish to slow their heart rate in response to a thermal stimulus. As a conditioning stimulus (CS), the temperature of the stimulus stream, water directed either to the back or to the mouth, was abruptly reduced 5° below ambient. It was followed by the unconditioned stimulus (US), a momentary cessation of the gill-perfusion flow, to which the fish responded (unconditioned response, UR) with an immediate lull in heart beat followed by several irregularly spaced beats. During testing, heart rate and stimulus temperature were continuously monitored and recorded. Fish were generally tested for 30 trials; intertrial intervals were 2–4 min. During the intertrial interval, temperature of the streams were 24°C, the same as the holding tanks.

During a trial, temperature of the stimulus stream was reduced by pumping iced methyl alcohol through the outer jacket of a counter-current heat exchanger. The stimulus stream flowed through the exchanger's inner tube, a 10-m segment of 2-cm copper water piping. We felt that the fish would not be stressed by 2 hr exposure to copper leached from the exchanger during the water's brief transit, an unwarranted assumption since fish that respired copper-contaminated water (the mouth-stimulated group) did not survive as well as the back-stimulated group.

Because spontaneous decelerations occurred, the frequency of responses during the intertrial period was compared to frequency of responses during the times when the temperature was decreasing but before the gill perfusion water was shut off (Dizon *et al.*, 1974). A responding fish should exhibit a higher frequency of response during the stimulus period than during the intertrial.

RESULTS AND DISCUSSION

Figure 1 shows good examples of heart-rate deceleration (possibly a conditioned response, CR) in response to a temperature stimulus (CS) delivered to the oral–branchial cavity. The responses occurred at about 2°C below ambient. In the second panel, the gill perfusion water was shut off (US) at 5·2°C and another response occurred (UR).

To obtain an estimate of thresholds, responses for each fish were grouped by 1°C intervals (0–1°, 1–2°, 2–3°, 3–4°, or 4–5°). Frequency of response for each fish was determined as a function of stimulus stream temperature by dividing the number of responses in each interval by total time for that interval. The median frequency of response for all fish in each treatment group and 95% confidence limits on the median (Mood & Graybill, 1963) were determined for each temperature interval (Fig. 2). As observed previously with increasing temperature stimuli (Dizon *et al.*, 1974), frequencies of response varied significantly with temperature only for the mouth-stimulated fish (Friedman

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‡ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

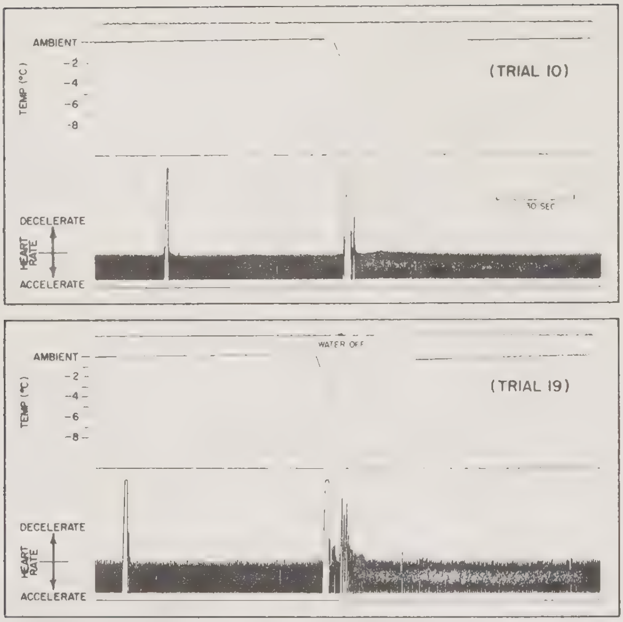

Fig. 1. A recording from a skipjack tuna showing abrupt deceleration of heart rate accompanying a decrease in temperature of the gill perfusion water and prior to reinforcement.

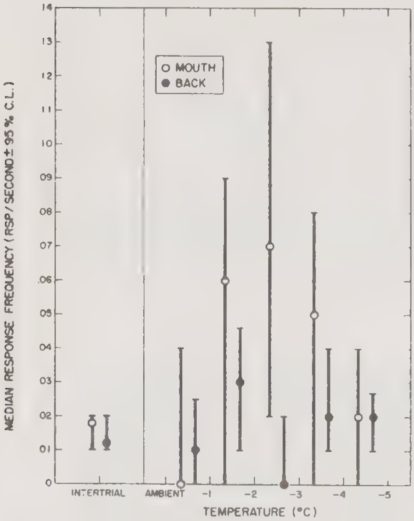

Fig. 2. Median response frequencies and 95% confidence limits of skipjack tuna before temperature stimulation (intertrial period) and during temperature stimulation by 1°C intervals. Open circles: temperature stimulation delivered to oral-branchial cavity (mouth), $n = 17$. Closed circles: temperature stimulus delivered to the dorsal, anterior body surface (back), $n = 18$.

two-way AOV by ranks, $P < 0·05$; Siegel, 1956). Median response frequency of the 17 mouth-stimulated fish was maximal in the 2–3°C interval but an increase can be noted in the 1–2°C interval.

The threshold for response, 1–2°C below ambient, was similar in magnitude to that observed for skipjack tuna exposed to temperature increases (Dizon *et al.*, 1974) but was somewhat higher than those observed for other non-marine, non-pelagic fishes trained to discriminate temperature decreases. Thresholds for a decrease in temperature are available for trout (0·1°C) and catfish (0·5°C) (Bardach & Bjorklund, 1957) and a minnow (1°C) (Dijkgraaf, 1940). While 1°C is not a realistically low threshold, skipjack tuna are expected from these data to be equally sensitive to increases and decreases in temperature.

Combined data from all mouth-stimulated fish produced a significant difference (Kolmogorov–Smirnov one-sample test; Siegel, 1956) between response frequencies during trials and intertrials ($n = 17$, $P < 0·01$); combined data from all back-stimulated fish did not ($n = 18$, $P < 0·10$). The difference in probability levels (0·01 vs 0·10) implies that the fish responded more consistently to mouth stimulation than back stimulation. The median per cent increase in response frequency during temperature stimulation for each fish and each treatment was determined and tested with a one-tailed Mann–Whitney *U*-test (Siegel, 1956). Mouth-treatment scores ranked significantly above back-treatment scores ($U = 87$, $P = 0·025$). That is, thermal stimulation of the mouth was more likely to produce a response than like stimulation of the back. We suggest either: (1) Thermal stimuli delivered to the mouth of the tuna are nociceptive, which would explain the reliability with which responses appear in restrained fish despite stressing conditions of the experiment. (2) There may well be a direct thermal effect upon the anterior brainstem

(Crawshaw *et al.*, 1973) when temperature changes occur within the mouth.

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Key Word Index—Temperature perception; Tunas; Thermoregulation; Classic conditioning.

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MINIMUM SWIMMING SPEED OF ALBACORE, *THUNNUS ALALUNGA*

Ronald C. Dotson[1]

ABSTRACT

Measurements of density and pectoral lifting area of albacore, *Thunnus alalunga*, were made and compared with those previously described for yellowfin tuna, *Thunnus albacares*; bigeye tuna, *Thunnus obesus*; and skipjack tuna, *Katsuwonus pelamis*. Albacore have densities within the range of yellowfin tuna of similar size. The pectoral lifting area of albacore was always greater than skipjack tuna but similar to yellowfin tuna and bigeye tuna for fish less than 70 cm long. Larger albacore had increasingly larger fins than did the other species.

Minimum speed necessary for hydrostatic equilibrium of albacore was calculated and compared at 50 and 80 cm fork lengths to values calculated for the species above. Albacore minimum speeds were slower than those for skipjack tuna, similar to those of yellowfin tuna, and greater than those of bigeye tuna. Density variations of albacore, attributed to fat content and gas bladder volume, significantly affected estimates of minimum speed. Calculated speeds were slower than those estimated for albacore tracked at sea or estimated from tag returns.

Albacore tuna, *Thunnus alalunga* (Bonnaterre), being negatively buoyant in seawater, must swim continuously to maintain their position in the water column. The albacore's long pectoral fins help to compensate for their negative buoyancy by providing lift, thus lowering the swimming speed necessary to maintain hydrostatic equilibrium.

A model developed by Magnuson (1970) proposes that the minimum swimming speed of a scombrid fish is set by the necessity to maintain hydrostatic equilibrium rather than to provide adequate gill ventilation. When the lift provided by the pectoral fins necessary to compensate for the weight of the fish in water is estimated, the corresponding swimming speed can be considered the minimum necessary for the maintenance of hydrostatic equilibrium. This model was used by Magnuson (1973) to compare minimum speeds of several species of scombrid fishes that differed in pectoral lifting area, body shape, body density, and the presence or absence of a gas bladder.

The purpose of this paper is to 1) estimate the minimum swimming speed of albacore; 2) compare the minimum swimming speed of albacore with those for other scombrids; and 3) compare calculated minimum swimming speeds of albacore with swimming speeds estimated from sonic tracking of albacore at sea and from long distance tag returns.

MATERIALS AND METHODS

To compute the minimum swimming speed with Magnuson's (1970) model, it is necessary to determine the mass of the fish, the lifting area, the density of the seawater, and the density of the fish. As the peduncle keels probably provide negligible lift (Magnuson 1973), they are excluded in the computation of minimum speeds.

To determine the mass of albacore, 477 specimens caught between long. 130° and 140°W and lat. 30° and 40°N during June 1974 were weighed to the nearest gram on a magnetically dampened pan balance and their fork lengths recorded to the nearest millimeter. Specimens were weighed and measured within 15 min after capture.

A regression $\ln M = \ln a + b(\ln L)$, where M is mass in grams and L is fork length in millimeters, was fitted to the length-mass data. The resultant equation was

$$M = 4.514 \times 10^{-5} L^{2.8746} \tag{1}$$

with 95% confidence limits on the exponent from 2.8245 to 2.9246.

The total pectoral lifting area (A) is equal to the projected surface area of the pectoral fins plus the projected body area between them, due to their analogy to wings in which the pressure distribution set up by the wings extends across the fuselage (Magnuson 1970). The pectoral lifting area was determined by tracing the outline of the

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detached left pectoral fin on a piece of paper having a thickness of 0.25 mm. The outlined form was cut out and weighed to the nearest 0.01 g on a balance. Projected area was calculated from a ratio of the paper weights to a standard, and doubled to account for the other pectoral fin.

Thirty-three 100 cm^2 pieces of the paper were measured with a micrometer and weighed to determine the affect of variations in paper thickness and cutting accuracy on the calculations. The thickness of the paper varied less than 1% around the mean, and cutting accuracy varied by ±2%. The affect on calculations of pectoral lifting area was, therefore, assumed to be negligible.

The projected body area between the pectoral fins was determined by multiplying the body width at the pectorals by the width of the pectoral fin at its point of attachment to the body as measured on the fresh fish. Pectoral fin lifting areas were determined for 42 fish caught in the area described above and for 8 larger fish caught off Oregon in October 1974. The following relationship was established between the lifting area (A in square centimeters) and the fork length (L in millimeters):

$$A = 4.7351 \times 10^{-6} L^{2.6727}. \tag{2}$$

Albacore observed cruising under the baitboat kept their pectoral fins extended continuously at a sweepback angle of approximately 45°. The tips of an albacore's fins are also not rigid, and the effect of this on the lifting capacity of the fin has been ignored.

A water density (D_e) of 1.025 g/ml was determined from temperature and salinity data from the offshore region described above. This also equalled the mean water density within the nearshore albacore fishery.

Fish densities were determined for three groups of fish: group 1—seven fish caught during June 1974 in the offshore region; group 2—14 fish caught 60 miles south of San Diego on 23 July 1975, presumably 2 wk after they appeared off the coast; and group 3—37 fish caught on 13 September 1975 in the same region as group 2 but assumed to have been near the coast for 2 mo.

The group 1 fish were frozen immediately after capture and, when returned to the laboratory, thawed and weighed on a spring balance while suspended in seawater to determine the density of the fish in seawater (D_f).

Fish from groups 2 and 3 were weighed in seawater on a pan balance immediately after capture and their densities in seawater determined.

VARIATIONS IN DENSITY

The density of group 1 fish (Figure 1) is well within the range of those determined for fresh fish of similar size indicating that freezing and thawing probably had negligible affect on density determinations. All specimens were caught on or near the surface by jigline or rod and reel, and there was no difference in density attributable to one method of capture over the other.

Rough estimates of the development of the gas bladders of 21 fish in group 3 were made immediately after other measurements were completed. In specimens less than 56 cm FL (fork length), the bladder was small (approximately 1 cm wide and 8 or 9 cm long) and contained little or no gas. In specimens 60 to 70 cm FL, the bladder was approximately 5 cm wide and 16 cm long and filled with gas to a depth of 4 or 5 cm. Fish over 80 cm FL had bladders approximately 30 cm long and 10 cm in diameter which occupied a large volume of

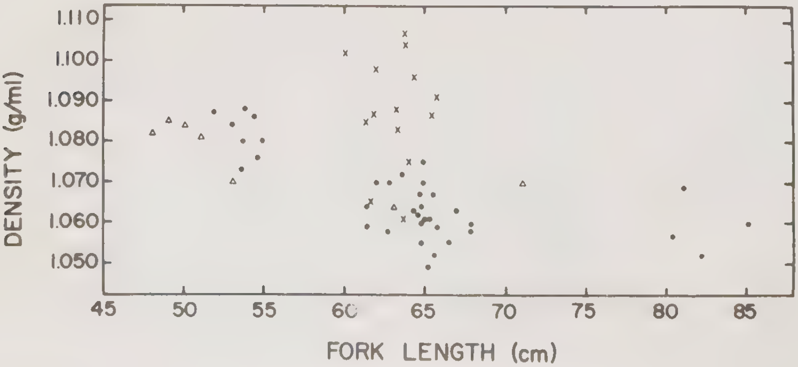

FIGURE 1.—Computed densities for three groups of albacore: group 1 (triangles); group 2 (crosses); and group 3 (dots). See text for explanation of groups.

the gut cavity. All developed gas bladders appeared full with two exceptions, and these may have been damaged during capture or dissection.

Seven albacore caught in September with fork lengths of 63 to 68 cm were examined to determine the effect of the gas bladder on density. Gas was removed from the bladder by a cannula (inside diameter = 1 mm) which was inserted through the ventral surface of the body while the fish was submerged in seawater, and the fish was then weighed while still submerged. The mean density increase with gas extraction was 0.007 g/ml (Table 1). Although this is probably a conservative estimate, the difference in density calculated before and after gas removal is used as the effect of the gas bladder on fish density. In an albacore less than 56 cm FL, the small gas bladder is not expected to affect density whereas the large and fully developed gas bladder of albacore greater than 80 cm FL should reduce density to a greater extent than was measured on the smaller fish above.

Densities of group 2 fish were considerably higher than those of similar size fish in groups 1 and 3 (Figure 1). Seasonal variations in density due to changes in fat content have been described for other pelagic species by Aleev (1963). Mass estimates were calculated from the length for each fish in all three groups using Equation (1), and compared with the observed values. The mean of the observed values for group 2 fell 403 g below the estimate from the regression line, ranging from 172 g greater to 999 g less. Because fish in group 2 had apparently just migrated into the area of capture, presumably from the central or western Pacific, the loss in mass was assumed to have been caused by the utilization of fat during migration. Group 1 would not yet have utilized this fat, and group 3 is assumed to have added fat by feeding in the rich coastal waters.

The densities in group 2 were recomputed on the assumption that the mass difference between the individuals and the regression curve is attributed to fat loss. An equation was developed by Magnuson (1970) relating the density (D_f) of a scombrid without a gas bladder to the percentage (P) of the total body weight that is fat. The equation

$$D_f = 1.100 - 0.0017\,P \qquad (3)$$

was used to recompute densities for the fish in group 2. The effect of the gas bladder on density was assumed to be 0.007 g/ml because fish in group 2 were in the same size range as the above fish for which gas bladder measurements were taken. This value was added to the observed density and the percentage body weight in fat calculated. The difference in mass (assumed to be fat loss) of each individual was then added and new densities determined with the increased percentage of body fat. The density effect of the bladder was subtracted from this value to yield a density adjusted for fat loss. When determining fat content in the fish, the density effect of the bladder was taken into account, except for those fish with measured densities greater than 1.100 g/ml, which is the level Magnuson (1970) chose as the density for a scombrid without a gas bladder. Fish with densities greater than 1.100 were assumed to have empty or damaged gas bladders, and the density difference due to the gas bladder was subtracted from the recomputed density.

Recomputed densities of group 2 are plotted in Figure 2 with the measured densities of groups 1 and 3. The close fit of the recomputed densities appears to support the assumption that fat content and gas bladder volume can account for the disparity in densities observed for group 2 in the original data. Density values are, therefore, expected to vary considerably depending on the development and condition of the gas bladder and the fat content of the fish when it is caught.

DETERMINATION OF MINIMUM SPEED

To estimate the minimum speed for hydrostatic equilibrium, it is necessary to calculate the amount of lift a fish must produce. The lift (L_f) required by a scombrid to attain hydrostatic equilibrium, expressed in dynes, is determined from the relation (Magnuson 1970)

$$L_f = M\left[\left(1 - \frac{D_e}{D_f}\right) 980\ \text{cm/s}^2\right]. \qquad (4)$$

When the lift is assumed to be provided solely by the pectoral fins, and the coefficient of lift for the pectorals is assumed to be 1.0, then the equation for minimum swimming speed becomes (Magnuson 1970)

$$V = \left[\frac{L_f}{D_e/2(A)}\right]. \qquad (5)$$

Calculations of minimum swimming speed from

TABLE 1.–Density changes in albacore following gas bladder deflation and resultant effect on estimation of minimum speed.

Characteristic	Albacore no. 1	2	3	4	5	6	7	Mean
Fork length (mm)	627	643	646	648	653	679	679	654
Density with gas bladder (g/ml)	1.058	1.063	1.062	1.055	1.061	1.060	1.058	1.059
Density without gas bladder (g/ml)	1.063	1.069	1.068	1.058	1.067	1.067	1.071	1.066
Change in density due to gas bladder (g/ml)	0.005	0.006	0.006	0.003	0.006	0.007	0.013	0.007
Minimum speed with gas bladder (cm/s)	45.0	48.6	48.7	44.5	49.8	47.3	47.9	47.4
Minimum speed without gas bladder (cm/s)	47.9	52.2	52.4	46.5	53.9	51.7	56.3	51.6
Change in minimum speed due to gas bladder (cm/s)	2.9	3.6	3.7	2.0	4.1	4.4	8.4	4.2

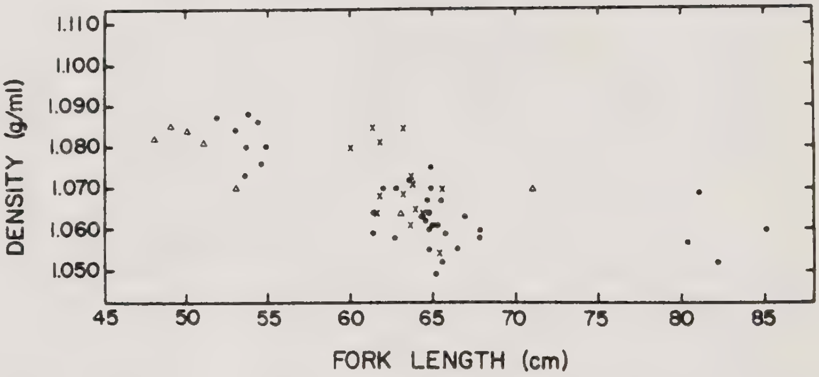

FIGURE 2.–Computed densities for three groups of albacore with group 2 densities (crosses) recomputed after correction for fat loss. Recomputation of group 2 densities is explained in the text.

this equation assume 100% extension of the pectoral fins.

The mass of the fish (M) and the lifting area (A) can be calculated using Equations (1) and (2), respectively. The density of the environment (D_e) is 1.025 g/ml. If we use $M = 2{,}540$ g, $D_f = 1.082$ g/ml, $A = 77.4$ cm^2 for a 50-cm fish, the calculated minimum speed V is 54 cm/s.

Density variations due to fat content and gas bladder volume can affect the minimum swimming speed necessary to maintain hydrostatic equilibrium. For a 65-cm albacore, a loss of 10% of its body weight in fat would result in a 10% increase in minimum speed. Loss or emptying of the gas bladder results in an 8% increase in minimum speed. Minimum speeds calculated from data on fish with full gas bladders and in good condition are therefore considered to be the minimum obtainable while retaining hydrostatic equilibrium.

COMPARISON OF MINIMUM SPEEDS OF FOUR SCOMBRIDS

Minimum speeds were calculated for albacore; yellowfin tuna, *Thunnus albacares*; bigeye tuna, *T. obesus*; and skipjack tuna, *Katsuwonus pelamis*, at fork lengths of 50 and 80 cm. The speeds are given in Table 2 with the density, mass, and pectoral lifting area used in the computations.

The minimum swimming speed of albacore decreases from 57 cm/s when they are 50 cm FL to 45 cm/s at 80 cm FL. The decrease is a direct result of the allometric growth of the pectoral fins (Yoshida 1968) and the gas bladder (Gibbs and Collette 1966). The gas bladder of albacore does not have significant development when the fish is less than 55 cm long, but has considerable volume at a fish length of 65 cm, and apparent complete development when the fish has reached 80 cm FL (data, this paper). Combined with the increasing length of the pectoral fins, the result is a relatively

TABLE 2.–Estimated minimum speeds of four species of scombrids at fork lengths of 50 and 80 cm. The mass of the fish (M), pectoral lifting area (A), and density of the fish (D_f) used in the computations are also given.

Species	Fork length (cm)	M (g)	A (cm^2)	D_f (g/ml)	V (cm/s)
Thunnus alalunga[1]	50	2,588	77.40	1.082	57
	80	9,992	271.04	1.056	45
Thunnus obesus[2]	50	2,429	96.63	1.047	32
	80	10,825	233.80	[3]1.030	21
Thunnus albacares[4]	50	2,501	91.56	1.087	55
	80	10,338	220.50	1.050	47
Katsuwonus pelamis[4]	50	2,539	47.88	1.090	78
	80	12,567	137.20	1.096	107

[1] Data from present paper.
[2] M, A, and D_f from Magnuson (1973).
[3] Extrapolated value.
[4] M calculated from Chatwin (1959), A and D_f from Magnuson (1973).

abrupt drop in minimum speed between 60 and 70 cm FL (Figure 3).

Albacore and yellowfin tuna have very similar densities (Table 2), but the pectoral fins of albacore are smaller in young fish (Gibbs and Collette 1966), increasing very rapidly in size as the fish mature (Figure 4). Thus, small albacore have a faster minimum swimming speed than small yellowfin tuna, and albacore over 65 cm have a slower minimum swimming speed than the same size yellowfin (Table 2, Figure 3) assuming similar fat content and gas bladder development.

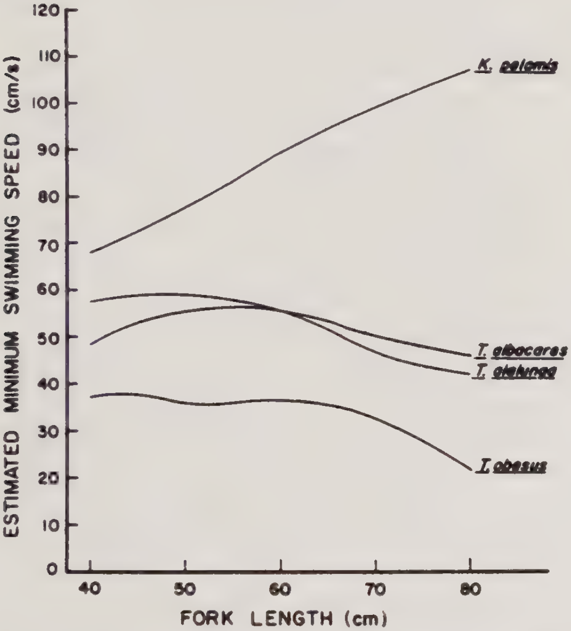

FIGURE 3.–The estimated minimum swimming speed of four scombrids using Magnuson's (1970) model for hydrostatic equilibrium.

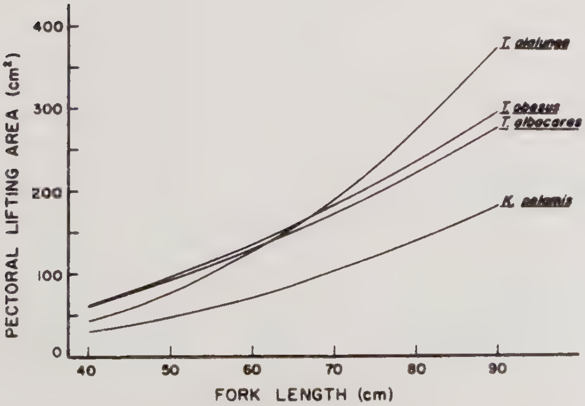

FIGURE 4.–Regression curves for pectoral lifting area (A) versus fork length. Curves for *Thunnus obesus*, *T. albacares*, and *Katsuwonus pelamis* are from Magnuson (1973). The curve for *T. alalunga* is from Equation (2) in the text.

Because bigeye tuna have a larger gas bladder than albacore and also have large pectoral fins, both of which grow allometrically (Gibbs and Collette 1966), their estimated minimum swimming speed is only half that of albacore at both 50 and 80 cm in length (Table 2).

The minimum swimming speed necessary for hydrostatic equilibrium of 50-cm albacore is 70% that of 50-cm skipjack and only 40% when each is 80 cm long (Table 2). Unlike albacore, skipjack have no gas bladder and always have small, short pectoral fins; therefore, skipjack tuna must swim faster as their mass increases in order to maintain hydrostatic equilibrium (Figure 3).

In Table 2 and Figure 3, density values for bigeye tuna were extrapolated beyond observed values and those of albacore were chosen from "fat" fish; therefore, actual values shown may not be exact, but the gross relationships among species are expected to hold true.

FIELD ESTIMATES OF ALBACORE SWIMMING SPEEDS

During August 1972, the National Marine Fisheries Service in cooperation with the American Fishermen's Research Foundation tagged six albacore with sonic tags and tracked their movements off the coast of Monterey Bay, Calif. (Laurs et al. 1972).[2]

Mean speeds observed during sonic tracking of three fish near 85 cm fork length were 95 cm/s during daylight hours and 62 cm/s during the night. These speeds are higher than the calculated minimum of 42 cm/s for a fish this size.

Each of two tagged albacore approximately 80 cm long, which were caught after a trans-Pacific migration, had a computed minimum or straight line speed (based on great circle route and time free) of 26 nautical miles/day or 55 cm/s (Japanese Fisheries Agency 1975). The calculated minimum speed of 45 cm/s is remarkably close to the estimated minimum migration speed of these two fish but could be an artifact of many interacting processes and events.

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MFR PAPER 1174

Monitoring the Ocean Environment

L. E. EBER

INTRODUCTION

Atmospheric and oceanographic conditions in the vicinity of the sea surface have historically been monitored by mariners and fishermen. From their observations has come much of our knowledge of the marine climate. Such observations, taken four times daily, recorded in weather logs and transmitted by radio to shore stations still constitute the primary source of information on surface conditions over the world ocean. This information is now supplemented by data from weather satellites which provide a major advance in global monitoring. The value of satellites for surveillance of atmospheric and oceanic conditions will increase greatly as sensor technology and processing techniques evolve.

There exists no systematic monitoring of subsurface conditions that can be considered comparable to surface monitoring. Subsurface temperatures are taken with XBT (expendable bathythermograph) systems installed on U.S. Navy vessels and on selected merchant ships which travel regular routes. Time-series data are provided by ocean station vessels (which are being withdrawn from service), and a few moored buoys and by sea-level stations at coastal and island locations. Sea-level data can give an indication of mean density in the water column in the vicinity of the station. Research vessels take subsurface observations of many kinds, but at times and places pursuant to particular objectives. Such reports must be considered as incidental to routine monitoring systems.

The basic purposes of monitoring the marine environment are to collect synoptic observations adequate for investigation of significant fluctuations in momentum and heat exchange and their effects on atmospheric and oceanic circulation, and on the distribution of relevant properties. Advances in the basic understanding of the ocean-atmosphere system have application to all activities affected by it, including transportation, military operations, harvesting and management of natural resources, recreation, etc. Particular applications may pose differing requirements upon the monitoring system with respect to time and space scales and to the properties monitored, although there are areas of overlap.

For many of these applications the existing monitoring system is considered inadequate.[1] The obvious shortcomings are the lack of surface observations outside normal shipping lanes and the general deficiency of subsurface observations, except along a few chosen tracks. Less obvious perhaps are the difficulties in making direct measurements of many important parameters and the uncertainties inherent in computing heat and momentum flux from existing observations. Not only are the semi-empirical formulas commonly used to compute these fluxes subject to question, but the actual parameter values used in the formulas (cloud amount; wind speed; and sea, air and dew point temperature) are subject to observational error. Nevertheless, in the sociopolitical, economic, and technological framework of today, there is no meaningful alternative to the existing data collection system from ships of opportunity (i.e., vessels whose primary mission is not collection of data) for large-scale monitoring of environmental conditions.

There are, however, many ways in which this system can be modified and supplemented to improve both the distribution and quality of environmental observations. Such augmentation of environmental monitoring will tend to be selective insofar as large-scale monitoring is supported mostly by government agencies, and the determination of where, when, and what to monitor is guided by an agency's objectives or mission.

The U.S. Navy, whose ships and shore stations contribute to the basic system, also supports supplementary monitoring from ships of opportunity to meet its needs for surface and subsurface data from areas not well covered by the basic system. It operates in both a direct mode, maintaining its own liaison with cooperating ships, and also indirectly through cooperation with marine-oriented academic institutions and with other government agencies, including the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS).

Academic institutions undertake the solution of a broad range of problems formulated to advance understanding of the ocean and atmosphere. They contribute directly to environmental monitoring through the activities of research vessels. They also contribute to the planning and improving of monitoring systems through investigation of space and time scales relevant to significant processes and events, development of instrumentation and methods of measurement suitable for large-scale monitoring, and through organization of observational programs needed to fill gaps in existing systems.

Weather satellites provide full global coverage of weather systems, over

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[1] The status of oceanographic monitoring efforts and a specification of needs for expansion are detailed in a recent report entitled "The ocean's role in climate prediction," available from the Ocean Affairs Board of the National Academy of Sciences, Washington, D.C.

Figure 1.—Environmental data received over National Weather Service teletype circuits are recorded on paper tape, transferred to punched cards, and inspected for quality control. The cards are then used to update environmental data files on disk for computer processing.

periods of about 12 hours, and partial coverage of surface conditions depending on cloud distribution. The National Environmental Satellite Service of NOAA, which operates this system, is primarily concerned with the sensing, reduction, and presentation of data, and has put much effort into analysis and interpretation of satellite data to facilitate user application.

In general, then, agencies and institutions draw selectively from the conglomerate environmental monitoring system according to their requirements and contribute to the total system by implementing subsystems, either on a unilateral or cooperative basis, to bolster weaknesses in particular mission-related areas. The primary purpose of this review is to describe some of the activities at the Southwest Fisheries Center (SWFC) which fall within that context. First, however, we will touch briefly upon a few of the attributes which might be considered desirable in an optimum monitoring system.

THE IDEAL SYSTEM

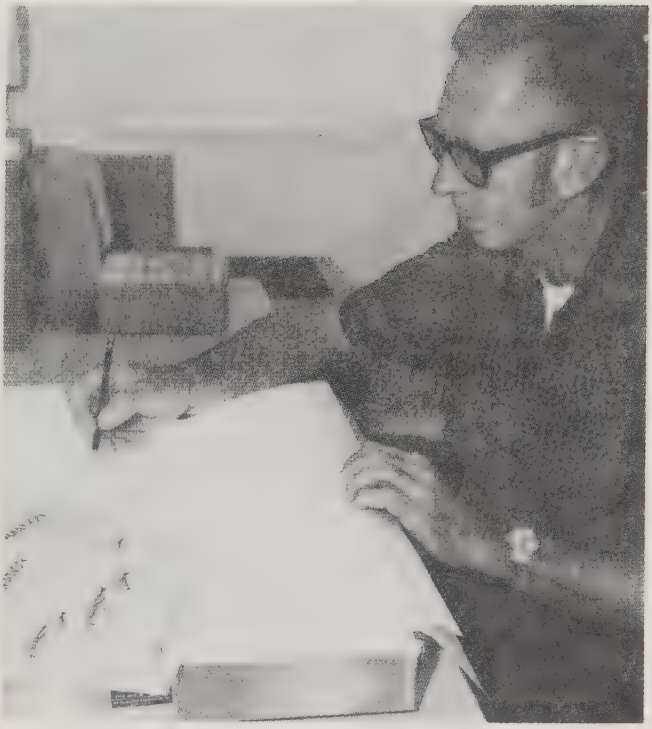
If sociopolitical, economic, and technological constraints are ignored, we can envisage the establishment of a World Ocean and Atmospheric Agency (WOAA) with effective capability for global monitoring. The WOAA could establish centers for collection, reduction, and analysis of all environmental data. The processed data could be loaded into a real-time data base accessible to user agencies and institutions through a time-sharing network. The real-time data base could be updated at intervals pertinent to the events or conditions being monitored. Data displaced from the real-time data base would be added to an historical data base in order to update time series and long-term means.

User agencies could select, manipulate, and further analyze data from either the real-time or historical data bases and, if appropriate, store results back into the system to be available to other users in the network. For example, generalized weather forecasts prepared by a world or national meteorological center might be retrieved, through the time-sharing network, at some particular service agency's center and tailored to the needs of that agency's constituency.

Consider the application of this conceptually ideal monitoring system toward achievement of efficient harvesting of living marine resources and effective resource management. The environment relates to these objectives in several ways. Thermal conditions, for example, establish the territorial range which particular species inhabit, and therefore delineate the fishing grounds. In temperate and colder zones, thermal conditions may have large seasonal variations which influence migration patterns and therefore delimit the fishing season. Deviations from normal environmental conditions affect the survival (abundance) and migration behavior (availability) of fish. Prognostic information on long-term trends in environmental conditions and on anomalous year-to-year fluctuations could be applied in planning and policy decisions by producers, processors, and resource managers. Analyses and short-term prognoses have application for tactical and operational decisions.

Oceanographic analyses applicable to fishing operations might include surface temperature and salinity, surface currents, location of surface convergence and divergence lines, subsurface thermal and salinity structure, and subsurface current structure.

Figure 2.—Sea surface temperature data application are edited, summarized, and plotted by computer. The final analysis of isotherms is drawn by hand. Such maps appear monthly in the publication *Fishing Information*.



For planning and management applications which do not require environmental information on a real-time basis, analyses of oceanic properties could be prepared for time spans associated with significant changes in a fishery during or between seasons. The selection of properties or fields to be analyzed could be based on either established or potential information value. Particular analyses with wide application might be loaded into a special products data-base in the time-sharing network and made available to nonagency users, fishery-related or otherwise.

Environmental research to advance basic understanding of processes and to develop applications could provide feedback into the monitoring system through refinement of the specification of time and space scales for observational networks, the properties to be measured and the observing techniques.

In summary, the principal elements of the idealized environmental information system are:

1) Capability for global monitoring of oceanic and atmospheric properties, circulations, and energy and momentum fluxes on time and space scales commensurate with significant fluctuations and events in the ocean-atmosphere system.

2) Global collection and data reduction and archival facilities in which historical and current environmental data bases would be maintained and made accessible to user agencies and institutions in a time-sharing network.

3) Partitioning of basic analysis and forecast responsibilities among user agencies according to their respective missions or objectives. Adaptation of basic outputs by other agencies to satisfy particular constituency requirements.

4) Global radio and satellite communications capability for coordinated transmission of environmental information products to ships at sea and remote land stations.

5) Provision for an environmental information products file in the time-sharing system for users with requirements for immediate access to the information.

6) Provision for timely preparation and dissemination by mail of time-averaged analysis and other products not in immediate demand.

7) Ongoing research to advance understanding of basic processes in the ocean-atmosphere system, to develop capability to predict anomalous fluctuations and, for fisheries management, to determine the effects on the fisheries of such fluctuations.

ENVIRONMENTAL MONITORING ACTIVITIES AT THE SOUTHWEST FISHERIES CENTER

Three principal activities concerned with contribution to and application of environmental monitoring which have been developed at the Southwest Fisheries Center (SWFC) are: 1) the radio facsimile (FAX) advisory program, 2) the publication of *Fishing Information*, and 3) the expendable bathythermograph (XBT) ship-of-opportunity program.

FAX Program

The FAX program evolved out of the need to supplement the existing environmental monitoring effort in the eastern tropical Pacific. Recognition of this need was stimulated by EASTROPAC, an international cooperative investigation of the eastern tropical Pacific, which was intended to produce information necessary for a more effective use of the marine resources of that area, especially tropical tunas. It was apparent that biological and physical properties alike were subject to significant spatial and temporal variations. It was also apparent that the tropical tuna fishing fleet afforded the best opportunity for obtaining environmental observations in the tuna habitat.

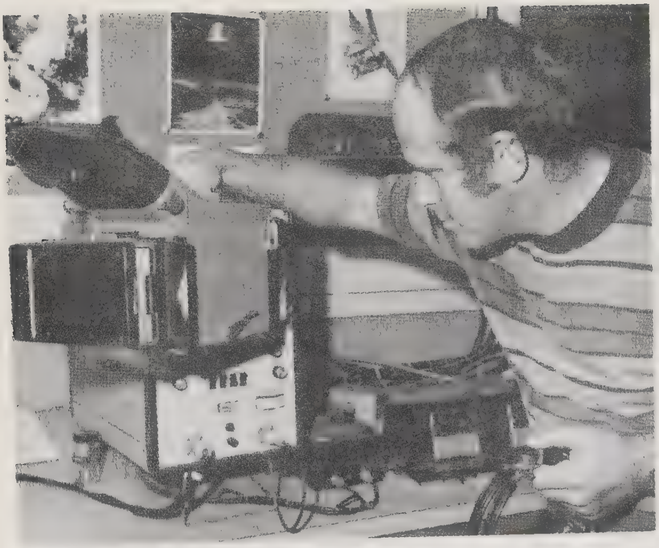


Figure 3.—Observations of cloud cover and weather phenomena transmitted from NOAA weather satellites can be received directly at the Southwest Fisheries Center. Application of satellite data to monitor ocean surface conditions is under development.

The NMFS's need for data from the eastern tropical Pacific was shared by the U.S. Navy's Fleet Numerical Weather Central (FNWC). Environmental data are used by FNWC to prepare analyses and forecasts of oceanic and atmospheric fields in support of U.S. Navy operations. Consequently, FNWC requires this data on a real-time basis.

The NMFS and FNWC recognized their mutual interest in enlisting the cooperation of fishermen for collection and transmission of observational data. They also recognized both an obstacle in securing such cooperation—that being a disinclination of tuna vessel captains to reveal their position on the fishing grounds—and a need to provide the fishermen with some incentive to take and transmit observations. The obstacle was removed through innovation of an encoding scheme for transmitting data messages which assured skippers of confidentiality with respect to their position. The incentive was provided in the form of wind, weather, and sea-state advisory charts, prepared especially for the area of the tropical tuna fishery and transmitted by radio facsimile from NMFS-licensed radio station WWD.

To implement the program, facsimile recorders were procured from government surplus and adapted for use with shipboard communications equipment. These recorders have been installed on more than 55 participating vessels under a reciprocal agreement providing for daily data transmissions from the fishing grounds. In addition, there are approximately 20 vessels in the program with privately owned units. Each vessel is furnished with its own unique encoding chart prepared at FNWC. The decoding keys are locked into the Navy computer, accessible only to the program which processes the observational messages. All participating vessels are expected to take and transmit surface weather observations, including wind speed and direction, weather, cloud cover, barometric pressure, air temperature, sea-surface temperature, swell direction, and wave height. Some 20-25 vessels in the tropical tuna fleet are equipped with XBT systems and report subsurface temperatures in the BATHY message format. The BATHY messages include temperatures and depths at significant points down to 500 meters, extracted from XBT analog traces. Maintenance of the XBT and FAX equipment is performed by SWFC personnel.

In practice, tuna vessels at sea begin transmission of weather and BATHY messages to station WWD each day about midafternoon. The messages are relayed via teletype line to SWFC and accumulated on a magnetic tape loop in the collect and transmit terminal unit of the Navy Environmental Data Network tie-line. At scheduled times, messages accumulated on the magnetic tape are sent over the tie-line to the computer at FNWC, decoded and processed for input to the FNWC operational programs. The decoded messages, along with other reports from the eastern tropical Pacific region, are sent back over the FNWC tie-line to SWFC and also to the NWS forecast office at Redwood City, Calif.

Data originating from tuna vessels, received at SWFC from FNWC, are punched on cards to be added to the environmental data base. Wind and sea-state parameters are extracted from these data and plotted on the current working charts used in preparation of the FAX advisories. Synoptic marine reports from merchant ships received over NWS meteorological teletype circuits also are used for this purpose, along with analyses and forecasts received over the NWS facsimile line and the FNWC tie-line and satellite pictures from NWS facsimile and from the SWFC direct readout system.

The weather advisory charts developed by the FAX program at the SWFC consist of a wind and weather forecast and a sea-state forecast. Prior to August 1974, these charts were transmitted from station WWD daily except Saturday and Sunday at about 4:15 p.m. The format and content of the SWFC FAX charts evolved through feedback from the fishermen. In addition to forecast wind speeds and directions, they depict the configuration of the Inter-Tropical Convergence Zone (ITCZ) and the locations of incipient tropical storms, which tend to develop along it. Such storms can intensify suddenly and pose a hazard to tuna boats which tend to fish in or near the ITCZ, trying to avoid strong prevailing winds outside but also wary of disturbances inside.

The National Weather Service (NWS) became a participant in the program in June 1974. A data line was established from the NWS forecast office, Redwood City, Calif., to radio station

WWD and to the SWFC, La Jolla, Calif., to be used for transmission of wind and weather and sea-state forecast charts prepared by NWS. Initially, the NWS charts were broadcast from WWD to the tuna fleet on weekends, to fill the gap in the SWFC transmissions, and recorded weekdays at the SWFC for evaluation and assessment of compatibility in format and in depiction of significant forecast elements.

Since August 1974, the NWS FAX charts have been broadcast from WWD daily. Surveillance of wind and weather conditions in the eastern tropical Pacific has been continued at SWFC, however, to insure that supplementary verbal advisories are broadcast from station WWD when appropriate, and to respond to direct requests from tuna vessels for information in specific situations.

In addition to the daily wind, weather, and sea state FAX advisories, three charts depicting ocean conditions are prepared at SWFC and transmitted by radio facsimile weekly. These are a sea-surface temperature analysis, a mixed layer depth analysis, and a sea-surface temperature difference chart which compares present conditions with those in the corresponding week of the previous year.

The success of the FAX program depends on continuing participation of a large number of tuna vessel owners and captains. The importance of taking observations, encoding them properly, and transmitting the radio messages must be stressed repeatedly. On the other hand, dialogue with the fishermen is also necessary to modify and adapt the advisory products as nearly as possible to their needs.

The weather logs and XBT records kept aboard the tuna vessels are collected by SWFC personnel when the vessels return to San Diego. Data taken on the fishing grounds but not received through the real-time transmission system are extracted from the logs and added to the environmental data base.

Figure 4.—Facsimile charts sent via land line from the San Francisco Weather Service Forecast Office are received simultaneously at the Southwest Fisheries Center and at radio station WWD, where they are recorded on magnetic tape. Visual inspection is made prior to transmission time for quality control.

Fishing Information

Charts of sea-surface temperature (SST) for the eastern north Pacific were published by the Honolulu Laboratory of NMFS (then the Bureau of Commercial Fisheries, BCF) from 1957 through 1959 in connection with a study of the distribution of north Pacific albacore. Responsibility for preparation of the charts was assumed by the BCF Tuna Forecasting Program, San Diego, Calif. in 1960, in order to provide up-to-date SST information to the tuna fishing industry, governmental fishery agencies, marine scientists, and meteorologists (Johnson, Flittner, and Cline, 1965). This program also undertook the compilation and publication of historical SST data back to 1947, in furtherance of studies on tuna environment (Johnson, 1961; Renner, 1963).

Initially, the SST charts were issued monthly for the region north of lat. 20°N and east of long. 180° and, during the albacore fishing season, semimonthly for the region of lat. 25° to 52°N and east of long. 136°W. Monthly SST plots for 1-degree squares were prepared for the eastern tropical Pacific between lat. 20° N and 20°S. The computation of the monthly and semimonthly mean temperature values, and the plotting of these values on base maps for analyses of the temperature fields, were done by hand. As emphasis shifted to automatic data processing and feedback from users identified additional needs for environmental information, the analyses were extended to include other regions and other properties.

Fishing Information now contains the following monthly charts: a) Sea surface temperature for the eastern north Pacific; b) Sea surface temperature for the western north Pacific; c) Sea surface temperature for the eastern tropical Pacific; d) Deviations from long-term means of a), b), and c); e) Difference between a) and the corresponding SST field one year earlier; f) Sea level pressure and resultant wind (both current month and long-term monthly means) for the eastern north Pacific.

Fishing Information also contains graphs of subsurface temperature structure along ships' routes from Hawaii to U.S. west coast ports, narrative descriptions of the significant features of the charts, and articles on the albacore fishery at the beginning and end of the albacore fishing season.

The semimonthly SST charts are now published year-round as the *Fishing Information* supplement. During the albacore fishing season, they are accompanied by the *Albacore Bulletin* which contains timely information on fishing conditions and on the progress of the fishery.

In addition to the charts listed above, a set of tabulations is produced each month which contains average SST's, air temperatures, dew point temperatures, sea level pressures, cloud amounts, and resultant winds for 5-degree squares. From these monthly averages of observed environmental variables are computed the principal components of heat exchange at the sea surface, including incoming radiation, reflection, back-radiation, evaporation, and sensible heat flux. The tabulations also contain deviations of each of the observed and computed variables from their respective long-term monthly means. These monthly tabulations are not routinely distributed, but are available for on-site use by local users. Also, a preliminary run of the 5-degree averages is made a few days before the end of each month for use by the Long Range Prediction Group of the National Weather Service. Cooperation with other organizations in this way offers potential benefit through progress in understanding and prediction of large-scale environmental fluctuations.

The computation of heat exchange components from monthly averages of observed environmental variables gives relatively gross estimates of heat flux across the sea surface. Although there have been attempts to use such estimates in oceanic heat budget studies, their value for monitoring significant fluctuations has not been fully evaluated. To make the information more widely available, an 11-year series (1961-1971) of total monthly heat exchange has been compiled in chart form for the eastern north Pacific, and published along with monthly mean charts of each of the principal components averaged over the same period (Clark et al., 1974).

The principal source of data for the environmental charts prepared by the SWFC, other than reports from tuna vessels, are the 6-hourly synoptic ship's weather observations transmitted from ships at sea in the International Ship's Meteorological Code and collected by NWS. The system developed by the Tuna Forecasting Program in 1960 for processing the observations employed a computer program which produced printed SST summaries and other parameters at the end of each month. The summary values were hand plotted

Figure 5.—Advisory charts prepared for radio facsimile transmission are displayed for convenient reference along with environmental charts and satellite pictures received from the National Weather Service, and Fleet Numerical Weather Central.

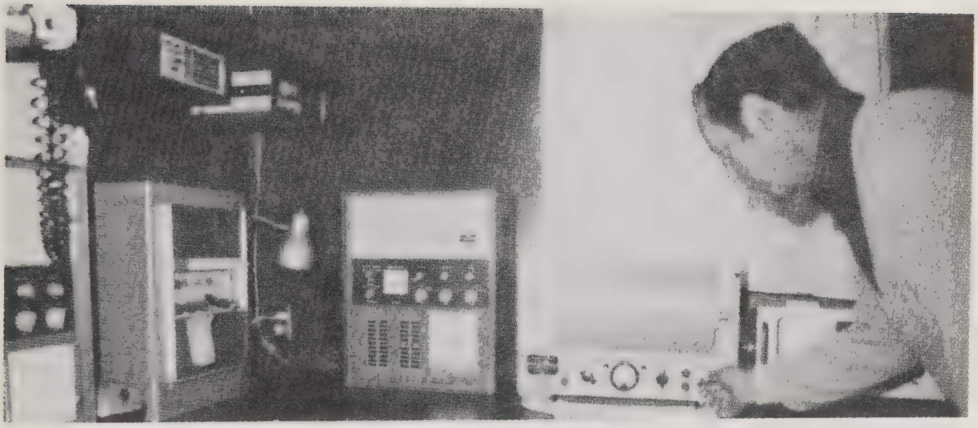


Figure 6.—Weather advisory charts can be received daily by fishing vessels such as this one equipped with radio facsimile recorders. Observational data received from the fishing vessels contribute significantly to the accuracy of the advisories.

and analyzed to prepare the environmental charts for *Fishing Information*. The original observations were saved on punched cards.

Subsequently, programs were added or modified to produce new outputs such as digital plots to replace those formerly done by hand, and special printouts formatted in a geographical grid for convenient reference. The present system provides for frequent update and ready accessibility of both current and past data on disk and magnetic tape files so that operational programs can be run on schedule and special analyses or plots for any time period and any specified region can be run as required.

Ship-of-Opportunity Program

This program was initiated to expedite utilization of a new instrument system (the XBT) capable of augmenting subsurface temperature monitoring and to apply the new system to create time series of subsurface temperature data along well-frequented shipping routes (Saur and Stevens, 1972). Such data are needed for the identification, quantitative description, and understanding of seasonal and nonseasonal changes in the subsurface temperature structure and heat content and of mass transports (through geostrophic estimation of currents) in the upper layers of the tropical and northeast Pacific Ocean. The program activities comprise three phases: 1) Data collection, in which observations of surface salinity and of vertical temperature profiles are made at 120-170 km intervals with expendable bathythermograph instrumentation aboard ships of opportunity; 2) Data processing, in which the observations are digitized, edited, printed for convenient reference, and added to the XBT data base for research; and 3) Data analysis, in which temperature-depth sections are prepared and the observations are analyzed to depict changes in subsurface ocean conditions.

The ship-of-opportunity program started in 1966 with a single ship, the Matson Navigation Company's bulk sugar carrier *Californian*, which made about two trips per month on the San Francisco-Hawaii run. The present program is considerably larger and, in 1974, involved three shipping companies and nine different ships.[2] During that year the program produced 52 sections between San Francisco and Hawaii, 27 sections between Los Angeles and Hawaii, 10 sections between Seattle and Hawaii, 2 sections between Alaska and Hawaii, 4 sections between Tahiti and Hawaii, and 4 sections between Samoa and Hawaii.

The program is conducted jointly with the NMFS Pacific Environmental Group, Monterey, Calif., where the digitization and computer analysis of subsurface temperature structures is performed and through which liaison with cooperating ships is supervised. Responsibility for the data analysis was transferred from SWFC to the Scripps Institution of Oceanography (project NORPAX) at the end of 1974. The program interfaces with FNWC interests in global monitoring of subsurface temperature on a real-time basis and with academic interests in understanding the processes of air-sea interaction and fluctuations in oceanic heat storage. The program receives support from FNWC, in the form of computer time and expendable probes, and from the National Science Foundation and the Office of Naval Research through project funding.

FNWC has supported the installation of XBT systems on merchant, fishing, and research vessels to supplement those on naval ships in order to obtain broad geographical coverage with sampling intervals sufficient to resolve large-scale oceanic features. For definition of mesoscale eddies, which have come under recent investigation by oceanographers and may be important in connection with transient ocean fronts, much finer sampling is required. Such sampling can be carried out from merchant ships only when project observers are aboard. The NMFS program has endeavored to maintain an intermediate sampling interval sufficient to identify transition zone characteristics between water masses and to reveal significant fluctuations along repeated tracks.

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[2] Matson Navigation Company, Chevron Shipping Company, and Pacific Far East Line. Mention of trade names, commercial products, or firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

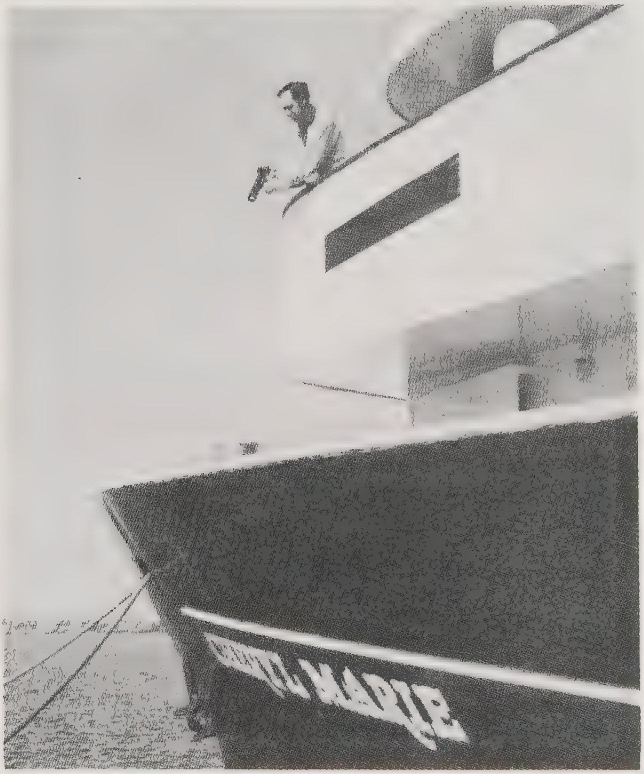

Figure 7.—Some fishing vessels are equipped with expendable bathythermograph systems. Temperature-sensing probes, released from a hand-held launcher, send data back to the vessel through fine conductor wires as they descend through the water.

Ancillary Information Sources

In establishing capability for monitoring environmental conditions of concern to fisheries, SWFC has become an acquisition center for real-time environmental information in a variety of forms. Analyses and forecasts of subsurface, surface, and upper air conditions are received daily over the FNWC tie-line and plotted as charts on CalComp plotters. A similar array of products is received over the NWS facsimile circuit. The NWS circuit also carries gridded satellite pictures from polar-orbiting and geostationary weather satellites. These pictures are particularly useful in determining the location and configuration of the ITCZ and in following the development of tropical storms. SWFC also can receive pictures transmitted directly from the polar-orbiting satellites on nearby orbits which occur twice each day. The satellite pictures, oceanographic and meteorological analyses, and forecast charts are displayed on the chart board in the environmental data room for convenient reference by environmental analysts, other SWFC staff, and visitors. The daily proximity of current environmental charts helps the analyst become attuned to the time and space scales of real-time events and develop insights which can lead to new approaches in the investigation of the ocean-atmosphere system.

Weather satellites have great potential for ocean monitoring, and the National Environmental Satellite Service has spent considerable effort in the interpretation of data from scanning radiometer infrared sensors to determine sea-surface temperatures. Although significant problems exist, one of the foremost being cloud contamination, this effort appears certain to lead to useful application, and growing consideration has been give to ways of incorporating this information into the routine SST analyses. The SWFC has cooperated with the Inter-American Tropical Tuna Commission, through use of the direct readout satellite receiving system, in studies to evaluate the feasibility of using data from scanning radiometer sensors aboard NOAA satellites to discern oceanic fronts and to apply satellite data to problems of fishery oceanography (Stevenson and Miller, 1974).

APPLICATION TO FISHERIES

The purposes underlying SWFC's involvement in environmental monitoring, through the programs described in the preceding section, are to contribute to the development of the real-time fishery prediction capability and effective resource management. A fishery prediction and management system should accomplish two basic functions: 1) Help maintain the fishery at a level of abundance consistent with optimum yield and recoverability from adverse environmental conditions or excessive fishing pressure; and 2) Increase the efficiency of harvesting, through prediction of distribution and availability, in order to maintain a viable fishery that can deliver fishery products to the consumer at an economical and competitive price. By strengthening the total environmental monitoring effort in areas which are important to fisheries, the potential benefit of research in relationships between the environment and fisheries is enhanced.

Environmental data taken by tropical tuna fishermen on the fishing grounds in the eastern tropical Pacific during 1971-1974, as a direct result of the FAX program, are shown in Table 1. These data are being utilized in ongoing research on the relationship between environmental parameters and fishing success.

The FAX program contributes to the efficiency of harvesting by meeting the needs of tropical tuna fishermen for information on weather and ocean conditions. Interviews with 22 skippers and navigators were conducted between December 1973 and March 1974 to obtain the fishermen's evaluation of the

Table 1.—Summary of marine observations, 1971-1974.

Year	Weather	BATHY	Total observations	Boats
Collected by radio station WWD				
1971	[1]844	684	1.528	3-25
1972	2.150	498	2.648	39-53
1973	2.579	570	3.149	55-57
1974	2.178	408	2.586	61-63
Total	7.751	2.160	9.911	
Collected from weather and BATHY logs				
1971	—[2]	886	—[2]	3-25
1972	2.610	665	3.275	39-53
1973	5.167	1.160	6.237	55-57
[3]1974	3.265	616	3.881	61-63
Total	11.042	3.327	14.369	

[1] WWD did not collect weather observations on a regular basis until September of 1971.

[2] Weather observations from fishing vessels were integrated into the monthly deck of synoptic observations and not separately accounted for.

[3] 1974 figures are based on projections pending receipt of all of the 1974 data

FAX products. Nearly all of those interviewed indicated that they copied the FAX charts every day, if possible, and listened to the verbal advisories broadcast on weekends when severe wind or weather conditions were expected.

The information regarded as most valuable is the location and expected movements of chubascos (tropical storms) and of extreme wind conditions such as occur in the Gulf of Tehuantepec. Sea and swell advisories and the sea surface temperature charts were rated next in value for aid in deciding when and where to fish. The mixed layer depth charts are being copied by most of the vessels, judging from the sample response, but were given a high value rating in only a few cases. These charts represent an effort to furnish environmental information to the fisherman on a provisional basis and thereby enlist his participation in developing the potential application of such information to fishing strategy. The charts also form a time series depicting weekly changes in oceanographic features, which may induce short-term variations in fish behavior and distribution.

The FAX program also provides a service to the albacore fishery through weekly transmission of sea surface temperature charts covering the albacore fishing grounds. This activity contributes to the joint research effort of the SWFC Albacore Research Investigation and the American Fishermen's Research Foundation (AFRF). These charts are copied by about a dozen vessels equipped with FAX recorders by AFRF. As with the tropical charts, they provide the fisherman with environmental information applicable to fishing strategy, and also support the work of the albacore investigations in modeling the albacore fishery.

The series of monthly and semimonthly charts of sea surface temperature and other environmental fields, published in *Fishing Information* and its *Supplement*, go back as far as 1960. They are sent to a distribution list of some 1,196 individuals, organizations, institutions, and agencies, some of whom receive copies for further distribution. In order to assess the impact and utilization of these charts, recipients were asked to fill out and return a brief questionnaire distributed with the November 1973 issue. A total of 575 questionnaires were returned. They reveal the following breakdown by user classification:

User classification	Percent of total returns
Commercial fishermen	38
Processors and distributors	3
Sport fishermen	9
Fishery managers	10
Marine scientists	16
Teachers	10
Other	14

The last category includes meteorologists, military oceanographers, marine suppliers, librarians, trade journal publishers, and others. The survey revealed that the charts are used primarily for fishing strategy by commercial and sport fishermen, for planning by processors, for fishery research by fishery managers, and for environmental research and teaching by marine scientists, meteorologists, and educators. The survey indicated greatest interest in the SST charts for the eastern north Pacific; however, all of the environmental charts received favorable response.

Overall, the response to the questionnaire affirms that the program is accomplishing its original objectives. It benefits the industry by providing useful environmental information and contributes to potential advances in fishery prediction by benefiting environmental and fishery research. It should be noted that the preparation and distribution of environmental charts by this program is a unique undertaking, and to some degree, provides the only generally available source of quasi-current information on abnormal conditions, such as El Niño occurrences. The SWFC receives numerous inquiries during such anomalous events concerning the status and tendency of environmental conditions.

Although much work has been done on the relation of fish to environmental conditions, the problem has hardly been scratched. An intensive and long-range research effort must be sustained to determine the specific extent and nature of environmental control on the distribution, survival, and behavior of fish. A similar effort must be made to understand the forces that produce environmental fluctuations which may have significant effects on a population. Such efforts must be supported by a comprehensive monitoring of the ocean-atmosphere environment and by reliable assessments of sizes and locations of populations. Only when adequate descriptions of relevant environmental fields are available along with adequate descriptions of fish stock distribution, can the knowledge of environmental processes and of behavioral responses to such processes be applied effectively in a fishery prediction system to control the fishery.

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SONAR MAPPING IN THE CALIFORNIA CURRENT AREA: A REVIEW OF RECENT DEVELOPMENTS

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ABSTRACT

Some developments in the use of sonar to study pelagic fish schools are reviewed. Techniques for counting the number of fish schools per unit area, measuring their horizontal dimensions, determining their biomass, sizing individual fish within a school, and distinguishing northern anchovy, *Engraulis mordax,* schools from all others are discussed briefly. Acoustic observations of the distribution, behavior, sizes, and packing density of anchovy schools are reviewed.

INTRODUCTION

It is the intent of this paper to review the use of horizontally directed echo ranging devices (sonar) to study pelagic fish schools off the coast of California. Research objectives are reviewed and several papers by biologists at the California Department of Fish and Game (CDFG) and the Southwest Fisheries Center (SWFC) are discussed as they relate to a development of sonar research.

Sonar mapping is the process by which a sample transect of the upper mixed layer of the ocean is insonified by a ship proceeding at 9 to 12 knots. Echo returns are recorded or digitized for detection of aggregations of organisms thought to be mostly fish shoals. The primary measurements are the location of each school in the horizontal plane and the diameter of the school on an axis perpendicular to the direction of travel of the survey vessel (Figure 1). The method was first discussed by Smith (1970) and later by Mais (1974) and Hewitt, Smith and Brown (1976). Collectively the measurements yield the number of fish schools per unit area, the geographical distribution of fish schools within the survey area, and the relative proportions of the fish school sizes.

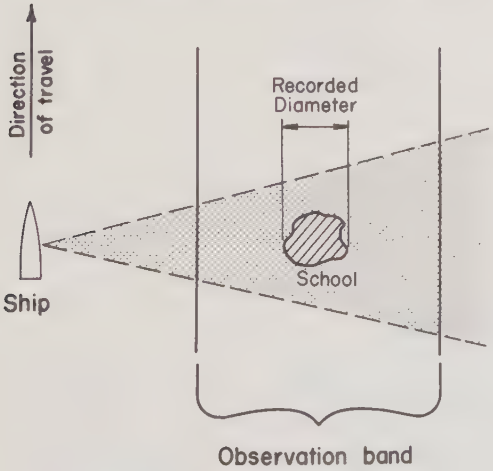

FIGURE 1. Plan view of the sonar mapping technique. Transducer is fixed at 90° to the ship's head rather than swept from side to side as in searching patterns.

Other measurements of the acoustic return have been demonstrated to be of use in estimating the biomass of a school, the size of the fish in a school, and in identifying schools of the northern anchovy, *Engraulis mordax,* in a mixture of fish schools. Unfortunately these measurements have not yet been feasible from a ship underway at full speed.

RESEARCH STRATEGY

The ultimate intention of the program to detect and determine fish schools by sonar is to develop a tool for pelagic fish stock assessment and to describe its precision. A secondary goal is to investigate the nonrandomness (or patchiness) of the spatial distribution of fish schools, particularly its similarity to distributions encountered when studying other life stages of the same group of animals; e.g., pelagic fish eggs and fish larvae.

In 1968, with these goals in mind, the development of the following capabilities were established as objectives of the research program:

1) To count the number of fish schools per unit of sea area,
2) To measure the horizontal dimensions of detected fish schools,
3) To estimate the fish biomass of any detected school,
4) to estimate the size of individuals constituting a school,
5) To distinguish northern anchovy schools from all other aggregations.

Progress toward the accomplishment of these objectives may be most clearly described with the use of a simple matrix which considers the five objectives, in terms of measurement capabilities, and the degree to which these capabilities may be considered practical operations (Table 1).

TABLE 1

Objectives of the Research at the Southwest Fisheries Center and the Degree to Which These Objectives have been Attained, as of 1975.

Objective	Phase I develop theory technique	Phase II demonstrate test feasibility	Phase III practical operation from a ship underway at 9-12 knots
1. Count fish schools per unit area	Accomplished	Accomplished	Automated and corrected for known biases
2. Measure horizontal school dimensions	Accomplished	Accomplished	Automated and corrected for known biases
3. Determine school biomass	Accomplished	Direct methods shown to be feasible indirect methods currently being calibrated	
4. Determine individual fish size	Accomplished	Acoustic techniques demonstrated as feasible	
5. Distinguish northern anchovy	Accomplished	Acoustic techniques demonstrated as feasible	

Counting Fish Schools and Measuring Their Horizontal Dimensions

The technique for determining the number of fish schools per unit area and their horizontal dimensions has been developed into a practical method and automated with a shipboard computer. All known biases have been investigated and proper corrections applied to the technique (Hewitt, Smith, and Brown, 1976).

A significant source of potential bias, encountered when enumerating schools with sonar, is the variation in effective range caused by internal waves. Temperature and salinity variations, due to internal waves, cause changes in the magnitude of sound velocity. While investigating the expected tidal period of these waves, Smith (1973) noted that variations of equal amplitudes occurred with periods as short as 5 minutes. The implication of short range spatial variations and the infeasibility of collecting coherent sound velocity profiles, led Smith to suggest a statistical approach to the estimation of a probable effective range.

Smith assembled long term hydrographic data for several subregions of the California Current area by month. He then assumed that no fewer than two sound velocity profiles per month-region stratum would be taken and sampling activities were allocated among regions and seasons to reduce the standard error of the mean sound velocity gradient to a uniform value. To illustrate the idea, a portion of his "allocation" table is reproduced here (Table 2).

TABLE 2

An Allocation of Sound Velocity Profiles Among Inshore Areas (0–80 miles from coast) by three regions and 4 months.

	Southern California inshore	Northern Baja California	Southern Baja California
January	2*	2*	3*
April	6	4	5
July	25	14	36
October	23	11	17

* The numbers indicate the number of profiles necessary to equalize the standard error of the mean sound velocity gradient in the upper 30 m.

Table 2 describes the number of sound velocity profiles required to equalize the standard error of the sound velocity gradient among regions and months. It may also be used to determine the optimum time of the year to conduct a sonar mapping survey in a particular region in terms of reducing the variability in effective range caused by thermal changes.

Smith further proposed the construction of a probability diagram to apply corrections to the numbers of targets received at various ranges and depths (Figure 2).

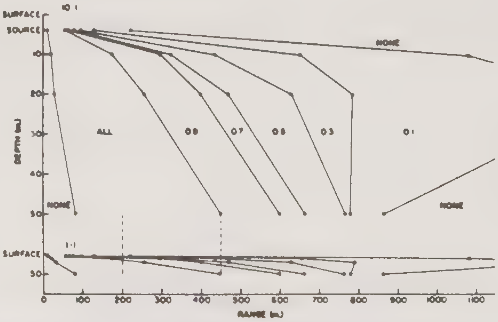

FIGURE 2. A pooled summary of 38 ray trace analyses of limiting range by depth by the probability of detection of −30 db targets (from Smith, 1973). Sound velocity profiles were obtained in October 1972 off the southern California coast.

Mais (1974) discussed, in some detail, his observations from enumerating and measuring fish schools, particularly those composed of northern anchovy. Mais reports the bulk of detected anchovy schools within 50 nautical miles of the coast and the most seaward school ever detected at 165 miles from shore. The north-south range is characterized by an ill-defined limit in northern California to a more abrupt southern limit 100 miles north of the southern tip of Baja California, with the bulk of detected schools off southern California and northern Baja California.

TABLE 3

Summary of Mais' (1974) Observations on Anchovy Schools and Their Constituents by Three Geographic Regions.

	Northern and central California	Southern California and northern Baja California	Central and southern Baja California
Distribution	5% of all detected schools. Bulk of schools within 0.5 miles of shore.	70% of all detected schools. Bulk of schools within 85 miles of shore; largest concentrations within 20 miles of shore.	25% of all detected schools. Bulk of schools within 15 miles of shore.
School types* encountered	I—most common, all seasons III—rare	I—most common, all seasons. II—encountered most frequently in the northern inshore portion of the bight, in the fall. III—encountered most frequently in the southern portion of the bight, in the spring. IV—rare. V—encountered year round in the inshore flats between Santa Barbara and Ventura. VI—encountered rarely in the late summer and fall in the inshore flats between Santa Barbara and Ventura. VII—encountered in the summer.	I—most common, all seasons. V—prevalent school type encountered in the summer and fall. III—encountered in the northern portion of region in the spring.
Age and length	Largest fish—most rapid growth	Slightly smaller fish than north and central California. Moderate growth—larger fish offshore, smaller inshore.	Slowest growth—shortest lived least maximum length.

* See text for explanation of school types.

Mais (1974) also reported a mean vertical school dimension of 12 m and both Mais and Hewitt et al. (1976) reported a median horizontal school diameter of 30 m. Mais further identified and described seven school patterns observed for the northern anchovy. The school types are briefly described below and summarized by region and occurrence (Table 3).

Type I: The most common school type encountered was 5 to 30 m diameter, 4 to 15 m thick (vertical dimension) and 9 to 18 m from the surface. These schools were the dominant type year-round but were detected most frequently during late winter and early spring. The schools were well delinated during the day, dispersing into a thin scattering layer at dusk. This was the only school type found to contain actively spawning fish. These schools were usualy wary and difficult to approach.

Type II: Large schools measuring 25 to 100 m in diameter, 12 to 40 m thick, and 0 to 55 m from the surface were encountered fall through winter over deep water basins and channels adjacent to the coast. These schools dispersed into a coarse scattering layer at dusk and reformed into distinct schools after midnight attaining their densest structures slightly before dawn. Time of schooling reformation occurred progressively later until January or February when it occurred after dawn. These schools were not wary and easy to approach.

Type III: Moderately large and dense schools, highly visible at the surface, and measuring 10 to 100 m in diameter and 12 to 40 m thick were encountered during spring and early summer over basins and channels within 20 miles of the coast. Samples from these schools suggested that the fish were in a postspawning stage.

Type IV: Large and dense schools were infrequently encounted at depths of 120 to 220 m along canyons and excarpments within 5 miles of the coast. These schools were observed to rise to the surface at dusk and form a heavy scattering layer. After midnight, surface schools would reform and submerge to daytime depths at dawn.

Type V: A loose and extensive scattering layer was occasionally observed during all seasons in the shallow flats (<100m) between Santa Barbara and Ventura, California, and in the summer and fall off central Baja California. The scatter was near bottom during daylight hours and formed a thin surface layer at night.

Type VI: Infrequently dense schools were observed in the shallow flats between Santa Barbara and Ventura during the summer and fall. these schools would form a scattering layer at dusk and regroup after midnight.

Type VII: A loose and extensive scattering layer was occasionally observed offshore of southern California during the summer months. Such concentrations were observed during daylight hours and over deep water.

Estimating Biomass

The determination of fish biomass contained in a school cannot at present be considered a practical operation; however, some progress has been made toward developing this capability. Anchovy school biomass is assumed to be a function of schooling densities. A theoretical model of school compaction has been developed to describe the maximum variability one may expect in school densities; two direct methods of sampling school compaction have been employed; and work is continuing with the aim of correlating direct and indirect measures of school compaction.

To gain an idea of school structure and resulting densities, an idealized model may be employed which can be used to compute the space required for a single fish when separated from its neighbors by a specified distance. The inverse of the resulting volume yields the number of fish which may occupy a unit volume for a given interfish spacing.

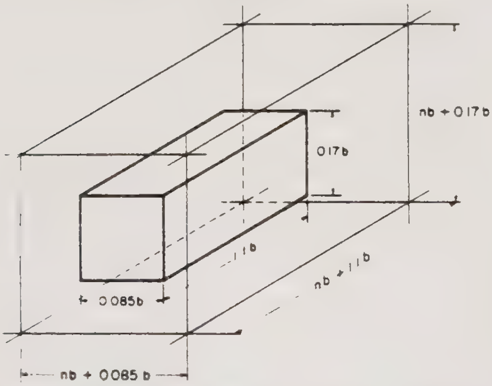

FIGURE 3. Idealized volume required by a single fish of standard length b in a school whose packing density is expressed by an interfish distance of nb.

The standard length, b, of an anchovy is used as the basic measurement. The fish is idealized as a rectangular solid whose dimensions are fractions of b. School structure is idealized by assuming that the fish's six nearest neighbors lie equidistant from the centers of the rectangle's six faces. If the interfish spacing is specified as some multiple of body length, nb, then the required volume for a single fish may be described (Figure 3). The volume, V_n, may be expressed:

$$V_n = (nb + 0.085b) = (nb + 1.1b)(nb + 0.17b)$$
$$= (nb)^3 + 1.355n^2b^3 + 0.2950nb^3 + 0.0159b^3$$

School density, D_n, is the number of fish which may occupy a unit volume for an interfish spacing of nb. D_n may be expressed:

$$D_n = (V_n)^{-1}$$

Using a standard length of 12 cm as typical of anchovy school constituents detected by sonar (Mais, 1974), a range of school densities may be calculated. The minimum spacing which may be attained without interference from the tail beat of adjacent fish is assumed to be 0.2b. The maximum spacing observed to be necessary to retain school integrity under ideal conditions is 10b. Densities have been determined using these maximum and minimum values and three intermediate points (Table 4). A maximum variation in anchovy school compaction of approximately 8,000 fold was estimated using this approach. While the model may be an oversimplification of school structure, it does provide an estimate of the scale of the parameter we are trying to measure.

TABLE 4

Interfish Spacing and Corresponding School Densities as Calculated from an Idealized Model

Interfish spacing in body lengths (nb)	Density fish (meter)$^{-3}$ (D_n)
10	0.51
7	1.41
4	6.66
1	217.08
0.2	4,219.40

Graves (1974) analyzed *in situ* photographs of anchovy schools in order to estimate various schooling parameters, including school density. Three-dimensional analysis of 10 photographs yielded school densities ranging from 50 to 366 fish/m^3. Although this represents only a small portion of the possible range of anchovy school compaction, Graves estimates that the technique may be useful over a range of 1,000 fold, i.e., 0.5 to 500 fish/m^3 (pers. comm.).

Another direct method of sampling school compaction was reported by Hewitt, Smith, and Brown (1976). Horizontal dimensions of 49 anchovy schools were measured acoustically and subsequently captured by commercial purse seiners. Assuming the school vertical dimension to be constant, a horizontal school area to biomass conversion factor was calculated by dividing the weight of the school by its detected area. Hewitt, Smith, and Brown (1976) used the mean of a distribution of this factor (Figure 4) to convert detected horizontal school area to fish biomass on a sonar mapping survey of the Los Angeles Bight. Assuming a vertical school dimension of 12 m and an individual fish weight of 20 g, these factors may be converted to school densities with a range of 0.52 to 533 fish/m^3.

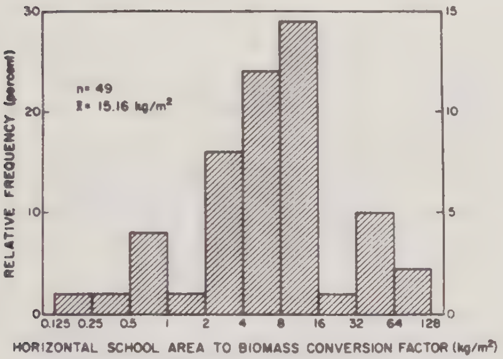

FIGURE 4. Distribution of horizontal school area to biomass conversion factors obtained from the charter boat experiment (from Hewitt, Smith, and Brown, in press).

The ideal method would be to correlate an indirect school measurement, in this case an acoustic parameter, with direct estimates of school compaction and thus establish a remote sensing technique for determining school density. Target strength, the ability of an object to reflect a sound wave, is an acoustic parameter easily measured with proper system calibration and signal digitizing equipment. When recording a peak value of target strength for each school, Hewitt, Smith, and Brown (1976) were able to describe a distribution range of 30 db (1,000 fold).

There are, however, several problems to consider when attempting to relate school target strength with school density. The target strength of a single fish has been shown to vary considerably with aspect by several experimenters (Cushing, 1973). One may expect this condition to exist in an aggregation of fish sharing a common directivity. Secondly, a fish school is neither a solid object nor a point source as considered in classical acoustic theory. Attenuation or absorption of the sound wave in a school must be considered as a complex function of fish aspect, reflection between fish and school density. Lastly, since target strength is measured by sampling a continuous variable (echo power), the calculation of a single value for each school is a function of the sampling frequency and averaging method employed.

Work is ongoing, at the SWFC, with the aim of correlating direct measures of fish school compaction (using camera and capture methods) with indirect measures (target strength). Schools are being insonified from several directions in an attempt to detect school aspect dependence of target strength estimmates. Target strength estimates are being made, using a variety of methods, from echoes which have been digitized at the smallest significant interval. The resulting distributions will be compared in a search to find the most meaningful one. The strategy is not to attempt to describe the interaction of a sound wave and an aggregation of fish, but to define an acoustic measurement, if any, which most accurately represents the school.

Sizing Individual Fish; Distinguishing Northern Anchovy

Holliday (1972, 1973, 1974) approached these related problems from an acoustician's point of view and demonstrated to biologists that meaningful information may be obtained by the application of acoustic theory. He investigated the frequency domain of echoes from pelagic fish schools by examining the resonance structure of echo returns (1972), and by studying the Doppler spread in echo energy (1974).

Using broad-band explosive acoustic sources and narrow-band spectral analysis, Holliday (1972) observed significant resonant structure in five schools. The schools were subsequently sampled and theoretical predictions for the resonant swim bladder response compared with the experimentally observed resonances. Correlation was made (Figure 5), and a method established for remotely determining the presence of swim bladders in an aggregation of pelagic organisms. A relationship between fish size and resonance frequency also was demonstrated. Holliday further suggested that the technique may be used for acoustic determination of weight or length distributions within a species and age determinations within a population.

The resonant frequency technique was modified and extended to underway operation at ship speeds up to 5 knots and described by Holliday in 1973. A towed arcer source, similar to those used for seismic profiling, and a towed hydrophone array were employed to detect significant frequency structure

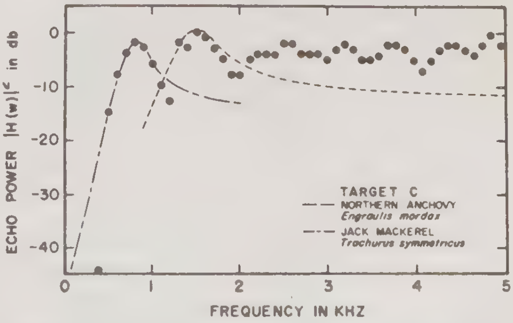

FIGURE 5. An example of the comparison between predicted and observed frequency structure in four echoes from a mixed school of jack mackerel and northern anchovy. The dashed lines represent predicted swim bladder resonance response and the dots represent observed values. The difference between the predicted curve and experimental points above 2 kHz is attributed to scattering from scales, bones, and flesh (Holiday, 1972).

in fish school echo returns (Figure 6). The structure was explained by resonant scattering from fish swim bladders.

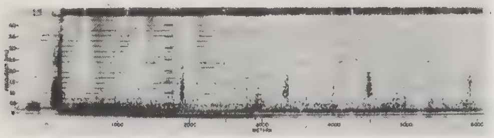

FIGURE 6. Frequency structure in fish schools echoes obtained from an underway survey vessel. Distance along the survey track is displayed on the abscissa; frequency is displayed on the ordinate; and echo energy is displayed as marking intensity (light marks representing less energy than dark marks).

In 1974, Holliday published a study of Doppler energy spread detected in echoes from pelagic fish schools. From the Doppler shift of side aspect echoes, the tail beat velocities of school constituents were calculated. Using Bainbridge's (1960) equation relating swimming speed, length, tail beat amplitude, and tail beat frequency, Holliday calculated the corresponding body lengths. These lengths agreed well with average fish lengths computed from observed school cruising speeds. When examining the Doppler spread from head and tail aspect echoes, Holliday was able to detect swimming behavior characteristics, particularly the accelerate-and-glide swimming behavior associated with northern anchovy and jack mackerel. By knowing the individual fish length and swimming behavior, it may be possible to distinguish northern anchovy from other common pelagic schooling organisms in the California Current area.

The two techniques described above are potentially valuable tools to the fisheries biologist. Additional work must be performed before they can be considered fully developed. In the case of resonance structure, information on the acoustical and physical properties of gas filled swim bladders as a function of depth, season, and geographic location must be obtained. With regard to Doppler structure, additional experimentation and confirmation of results is necessary.

Visual species identification is also possible by examining photographs taken with a free-fall camera[*] described by Graves (1974). The camera and method for quantifying photographs of fish obtained with it are valuable tools for confirming and calibrating remote sensing techniques.

ACKNOWLEDGMENTS

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[*] The camera system, commonly called the Isaac-Brown free-fall camera, was designed and built by John Isaacs and Daniel Brown at Scripps Institution of Oceanography.

CALIFORNIA UNDERCURRENT IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

In September 1974 hydrographic measurements were made to study the California undercurrent in the Southern California Bight. Three sections, extending 10 to 15 miles offshore from Del Mar, Oceanside, and Dana Point, were occupied with closely spaced STD stations. The observed distributions of properties suggested that an undercurrent (100–400 m) with a width of only a few miles was present at 5 to 10 miles from the shore.

INTRODUCTION

The California undercurrent, sometimes called the California countercurrent, is a narrow northward flow that is present below about 200 m and that extends along the coast from Baja California to Cape Mendocino (40°N) or farther north (Reid, Roden and Wyllie, 1958). Water transported by this current is of equatorial origin and characterized by high temperature, high salinity, low oxygen, and high nutrients as compared to California Current water farther offshore. On the temperature-salinity diagram undercurrent water is indicated by a high-salinity bulge centered near 150 cl/t of thermosteric anomaly (Wooster and Jones, 1970). Therefore, the distribution of the California undercurrent can be studied by mapping salinity on the 150 cl/t isanosteric surface. The 150 cl/t surface is 250–300 m deep and probably close to the core depth of the undercurrent. The area of the undercurrent indicated by high salinity (above 34.3°/$_{\infty}$) on this surface varies considerably from cruise to cruise (Wooster and Jones, 1970). Nevertheless, south of about 29°N (slightly north of Punta Eugenia) it has generally a large offshore extent ($>$200 miles) and is characterized by a distinct vertical maximum of salinity centered at about the depth of this isanosteric surface. North of 29°N the area of high salinity is limited to a very narrow strip next to the coast, and the vertical distribution of salinity does not exhibit a well defined maximum. (A similar distribution can be seen on the maps of the monthly mean salinity at 150 m prepared by Wyllie and Lynn, 1971.) Subsurface drogue measurements made by Reid (1963) off northern Baja California also indicate that the northward flow is narrow and found only within about 50 km of the coast. Because of the narrowness of the feature, it can easily escape from the network of the routine CalCOFI observations.

Recently, Wooster and Jones (1970) studied the undercurrent off Punta Colnett (31°N) with an array of closely spaced stations. Their measurements indicate that the northward undercurrent is only 20 km wide and bound to the continental slope.

STUDY AREA AND METHODS

In September 1974 the northward extension of this flow into the Southern California Bight, where the bottom topography is more complex, was investigated from the E. B. SCRIPPS during her first Southern California Bight study cruise (SCBS-1). Three sections, 20 miles apart, were occupied off Del Mar, Oceanside, and Dana Point (Figure 1). The station intervals were about 1 mile over the steep bottom slope from 100 m to 600 m and 3 to 4 miles in deep water farther offshore. On each station an STD was lowered nearly to the bottom. On seven stations oxygen samples were collected from Nansen bottles attached to the STD cable. No effort was made to directly observe the current velocity.

RESULTS

Property curves are plotted for two stations (Figure 2). Station 9 represents the distribution outside the undercurrent, and Station 7 represents the distribution in the undercurrent. There are clear differences in the distribution between the California Current and the undercurrent. At temperatures between 7°C and 10°C (depth 100–400 m), salinity at Station 7 is much higher and exhibits a well defined maximum centered near 150 cl/t of thermosteric anomaly. In the same temperature range, oxygen at Station 7 is about 1 ml/l lower than at Station 9.

The distributions of temperature and salinity are illustrated for the southernmost section off Del Mar (Figure 3). The shallow salinity minimum in the thermocline is derived from the California Current and is present everywhere on the section. The salinity maximum at about 300 m is associated with the northward undercurrent. The maximum is evident at Stations 10, 11, and 12, but Station 9 (shown in Figure 2) does not show any evidence of the undercurrent. The width of this high salinity water appears to be only 3 to 4 miles. On the temperature section, the isotherms for 8° and 9°C slope down toward the shore and suggest a northward geostrophic flow with its maximum speed at a depth of about 150 m, where isotherms are nearly level.

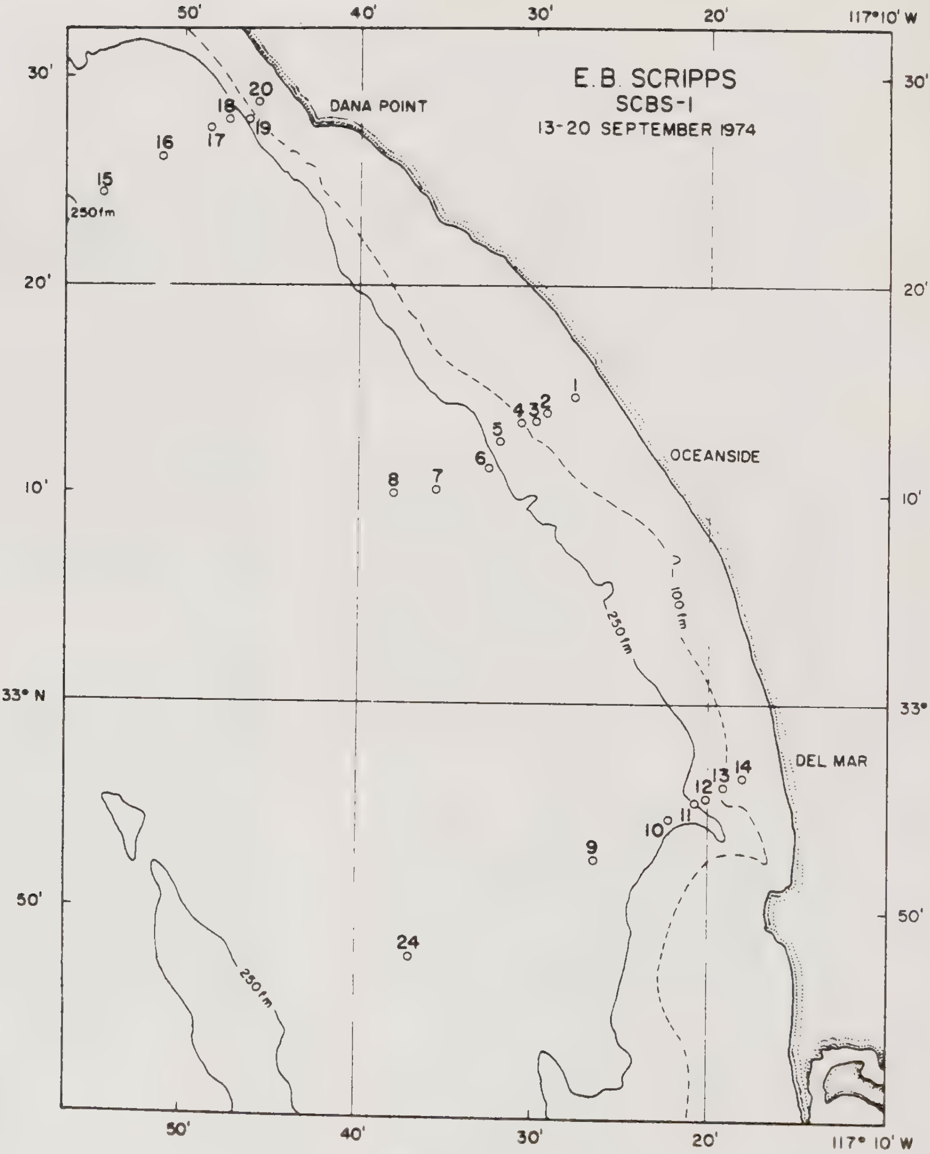
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FIGURE 1. Station positions.

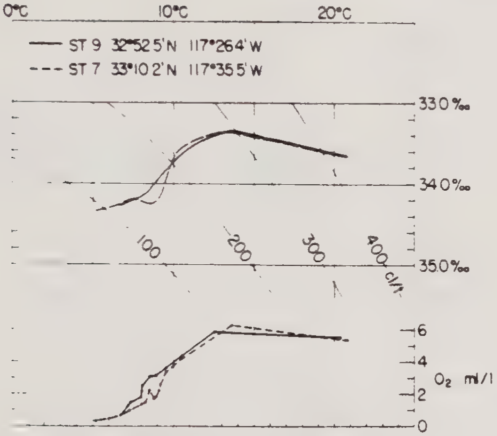

FIGURE 2. Temperature-salinity (top) and temperature-oxygen (bottom) curves (For station positions, see Figure 1).

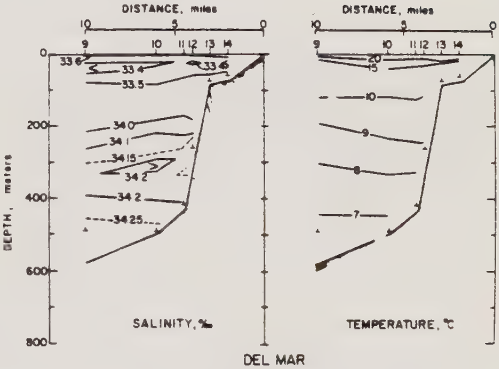

FIGURE 3. Vertical sections of temperature and salinity off Del Mar.

On the Oceanside section (Figure 4) 20 miles farther north, the salinity maximum is again apparent at Stations 7 and 8. The slope of the isotherms for 8° and 9°C between these stations is consistent with a northward geostrophic flow. The offshore portion of the undercurrent may have escaped from this section. Farther inshore, there is no evidence of the undercurrent except that isolated warm high salinity water is found at the bottom 30 m of Station 5 (not revealed by the isopleths in Figure 4).

On the northernmost section off Dana Point (Figure 5) there is no indication of high salinity water of equatorial origin. All stations show temperature-salinity and temperature-oxygen curves characteristic of the California Current.

In summary, the distributions of properties observed in September 1974 suggest that a northward undercurrent only a few miles wide was present at 100–400 m in the southern half of the study area. It was located at distances 5 to 10 miles from the coast. However, in view of the fact that Station 23, made 50 miles off Del Mar, and Station 24 (Figure 1) indicated the presence of high salinity water of equatorial origin, the main flow or a branch of the undercurrent may have occurred farther offshore. Clearly, more field work is needed to obtain a clear picture of the California undercurrent in the Southern California Bight.

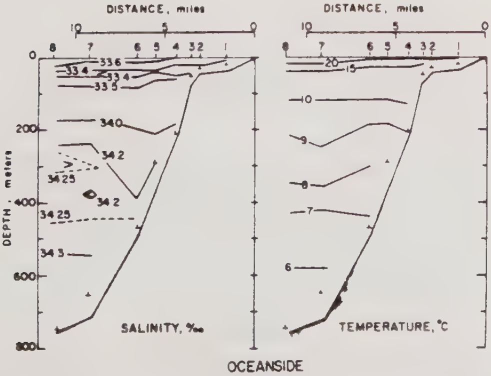

FIGURE 4. Vertical sections of temperature and salinity off Oceanside.

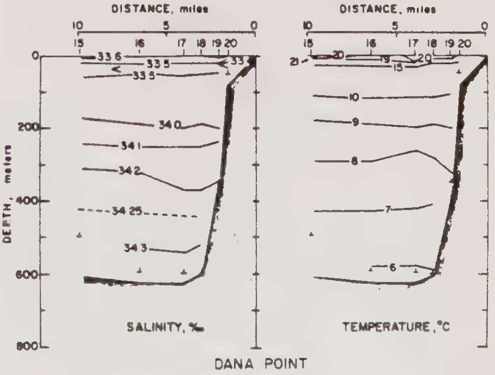

FIGURE 5. Vertical sections of temperature and salinity off Dana Point.

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SEDIMENT TRAP APPLICATIONS IN THE NEARSHORE REGION *

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ABSTRACT

The impact of a major sewage sludge discharge to Santa Monica Submarine Canyon off the Southern California coast has been studied using sediment traps to collect settling particulate matter in the vicinity of the discharge. The samples collected by the sediment traps revealed that both the fallout rates and the organic content of settling particulates are greatly influenced by the sludge discharge, but only in the immediate vicinity of the outfall. The particulate fallout rates and organic content were found to approach natural levels rapidly within a few kilometers of the discharge point. The discharged sludge was found to contribute less than 20% of the total particulate fallout and about 40% of the organic fallout to the Santa Monica Canyon ocean bottom.

INTRODUCTION

Coastal population centers have traditionally used the ocean as a disposal site for treated municipal wastewaters and, in some cases, for treatment plant sludges as well. The wastewaters and sludges contain a complex mixture of organic and inorganic substances in both dissolved and particulate phases. In general, a major portion of the wastewater constituents considered to be potential pollutants (heavy metals, chlorinated hydrocarbons, and oil and grease) are associated with the particular matter in the discharges. Consequently, a knowledge of the relatively immediate physical fate of the waste particulates is essential to an evaluation of the effects of wastewater discharges to the ocean. The use of sediment traps to collect samples of the settling particulate matter in the vicinity of wastewater outfalls is one method currently being used to gain such knowledge.

SAMPLING AND ANALYTICAL PROCEDURES

The sediment trap being used at the Coastal Water Research Project was designed by Andrew Soutar of Scripps Institute of Oceanography and consists of an inverted cone with a $0.05m^2$ collecting surface at the top and a removable sample container at the bottom. The entire device is supported on a tripod frame which holds the collecting surface approximately 2m above the ocean bottom. In 1974, four sediment traps were used to collect 29 samples at 22 stations over a period of about 7 months. The sampling period at each station ranged from 14 to 39 days and averaged 24 days.

The samples were refrigerated once on board ship and frozen upon arrival at the Project's laboratory the same day (samples that were to be analyzed the next day were kept refrigerated overnight). We determined the total amount of particulate solids in the samples and the organic content of the solids, using procedures described below. In the future months, we also will analyze the collected solids for chemical oxygen demand, oil and grease, trace metals, and chlorinated hydrocarbons.

Total particulate solids procedure

The samples were first centrifuged to concentrate the solids. The centrate was decanted and the wet solids transferred to a tared drying dish and weighed. The solids were dried at 80°C for 24 hours and weighed again. The sea salt content of the dry solids was estimated from the moisture loss, and this amount was subtracted from the weight of the dried solids (this correction ranged from negligible to 22%, depending upon the characteristics of the solids).

Solids organic content procedure

A small subsample of the dried solids was redried and weighed. This sample was then ashed at 550°C for 1 hour, cooled in a dessicator, and reweighed. The value for the weight lost in ashing was adjusted for the weight lost from combustion of the volatile components of the sea salts present. The adjusted weight loss was considered to be due to the combustion and volatilization of the organic matter present in the sample and was used as a measure of the organic matter.

STUDY DESCRIPTION AND RESULTS

The region selected for this study was the Santa Monica Canyon in Santa Monica Bay, California. The City of Los Angeles Hyperion Sewage Treatment Plant discharges 5 million gallons per day of a mixture of treatment plant sludges and secondary effluent at the head end of the canyon. About 131 metric tons of dry particulate solids per day are discharged through this system, and the organic content of these solids is usually between 60 and 70%. The objectives of the Coastal Water Project's study were to determine: (1) the rates of fallout of the discharged particulates at selected stations in the canyon region, and (2) the physical and chemical properties of the settling particulates at each station (limited to data on organic content at this time).

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* Contribution 34 of the Coastal Water Research Project

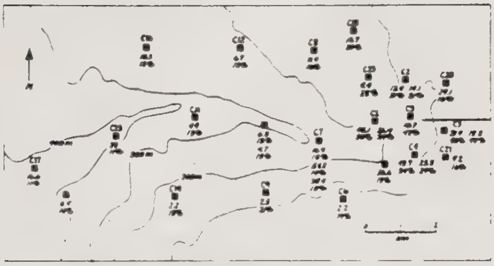

FIGURE 1. Santa Monica Canyon sediment trap stations, observed sedimentation rates (gm/m²/day), and organic content of trapped solids (%).

The calculated sedimentation rates ranged from 2.2 to 107 g dry solids m²/day, with the higher values occurring near the discharge point (Figure 1, Table 1). We took more than one sample at several of the stations to get an idea of the sedimentation rate variation from one sampling period to another: Five stations, C1, C2, C3, C4, and C10, were sampled twice, and one station, C7, was sampled three times. The observed deviations ranged from 2.5 to 54% of the mean station values, with an average deviation from the mean of 18%. As the quality and characteristics of the particulate matter discharged are fairly constant, these variations are probably due to changes with time in the water movement patterns in the canyon area. Variations in currents in the study area could change the speed and direction of discharged particulate transport and the quantity of resuspended surface sediments collected at any sediment trap station.

TABLE 1

Sediment Trap Data Summary 1974

Station	Sampling period	Total Solids		Organic content (%)
		Sample size (g)	Fallout rate (g/sq m/day)	
C1	5 Jun to 19 Jun	31.6	45.1	26.4
	19 Jun to 23 Jul	98.0	57.6	28.9
C2	5 Jun to 19 Jun	9.4	13.4	30.7
	19 Jun to 23 Jul	23.9	14.1	20.6
C3	5 Jun to 19 Jun	15.3	21.9	49.7
	19 Jun to 23 Jul	32.0	18.8	41.5
C4	5 Jun to 19 Jun	30.6	43.7	53.5
	19 Jun to 23 Jul	44.0	25.9	29.0
C5	23 Jul to 7 Aug	80.0	107.0	42.3
C6	15 Aug to 29 Aug	1.5	2.2	18.5
C7	4 Oct to 25 Oct	17.7	16.9	15.3
	25 Oct to 19 Nov	67.7	54.2	13.5
	19 Nov to 12 Dec	44.2	38.4	15.1
C8	23 Jul to 29 Aug	22.0	11.9	16.2
C9	29 Aug to 12 Sep	1.7	2.5	20.7
C10	4 Oct to 25 Oct	7.1	6.8	12.7
	25 Oct to 19 Nov	5.8	4.7	14.6
C11	29 Aug to 4 Oct	8.9	4.9	12.8
C12	29 Aug to 12 Sep	4.7	6.7	15.2
C13	29 Aug to 12 Sep	4.5	6.4	13.8
C14	12 Sep to 4 Oct	2.4	2.2	18.4
C15	4 Oct to 25 Oct	29.4	28.0	11.0
C16	12 Sep to 4 Oct	11.3	10.3	12.3
C17	12 Sep to 4 Oct	18.2	16.6	11.2
C18	4 Oct to 25 Oct	14.4	13.7	20.0
C19	12 Dec to 3 Jan	40.3	36.6	17.9
C20	12 Dec to 3 Jan	32.0	29.1	16.3
C21	25 Oct to 3 Jan	17.9	9.2	16.2
C23	19 Nov to 12 Dec	10.8	9.4	24.9

Current measurements were made at only one station, C17. Bottom currents at that station were recorded every 15 minutes for a period of 3 weeks in September 1974. The predominant currents recorded were downcanyon, with a net speed of 5.5 cm/sec. The highest current speed recorded was 32 cm/sec, and all currents greater than 25 cm/sec were downcanyon.

To compare the sedimentation rates obtained with the amount of solids discharged on the basis of mass per unit time, we assigned areas to each of the stations and estimated the total mass flux over the study area (69 km²). The estimated total solids fallout of 825 metric tons per day was 6.3 times the particulate solids discharge rate of 131 metric tons per day. The estimated organic solids fallout of 203 metric tons per day was 2.4 times the discharge rate of 85 metric tons per day.

The fact that there appeared to be much more particulate matter falling to the bottom of the canyon than was discharged at the head end may be the result of many factors. The sedimentation of marine particulate matter naturally occurring in the study area certainly accounted for some of the excess. No data have been found in the literature regarding sediment accumulation rates in submarine canyons. Emery (1960) studied sediment accumulation rates at several locations off the southern California coast and reported a net sediment accumulation rate of 3.4 g/m²/day for a station in Santa Monica Basin, his sampling station closest to the Santa Monica Canyon. This number corresponds closely with the sedimentation rates measured in this study at stations distant from the outfall. Andrew Soutar (Scripps Institution of Oceanography, pers. comm.) has measured the fallout rates of particulate matter in eight basins off southern California, using sediment traps similar to those used in this study. The rates he recorded range from 0.23 to 2.44 g/m²/day, with an average of 0.74 g/m²/day. His value for Santa Monica Basin is 0.69 g/m²/day, a factor of five lower than Emery's estimate.

It must be noted that the sediment traps collect falling matter. Thus, we are measuring particulate matter fallout rates, which may be quite different than sediment accumulation rates. Transport mechanisms such as bottom scour, which resuspends sediment and may greatly affect the sediment accumulation rate, are not operative within the sediment traps. The collection of resuspended sediments by the sediment traps is an unknown that could be significant. The speed of the canyon currents that we measured (9% of the observations were greater than 20 cm/sec) are sufficient to cause scour and resuspension of unconsolidated sediments (Hjulstrom 1939; Southard, Young, and Hollister, 1971). In the future, we plan to compare the sedimentation rates with estimated sediment accumulation rates since 1960, when the waste discharge began, to get an estimate of the importance of scour and resuspension as a transport mechanism in the study area.

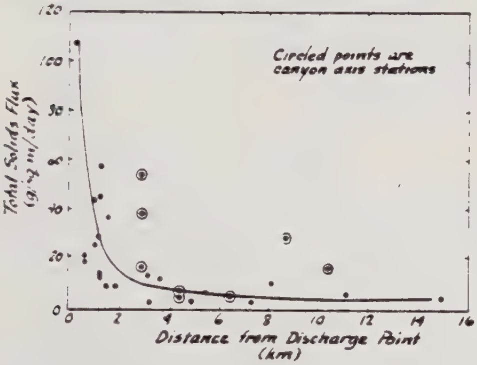

FIGURE 2. Observed sedimentation rates vs. location.

Most of the waste particulates discharged at the head of Santa Monica Canyon fall to the bottom within a few kilometers of the discharge point (Figure 2). A line indicating the trend of the data has been fitted by eye. The data are scattered about this proposed trend for a number of reasons, and some of this scatter appears not to be random. Beyond 2 km from the discharge point, the four obviously high data points are from canyon axis stations (C7, C15, and C17), and the three lowest points represent the three stations along the southern lip of the canyon (C6, C9, and C14). The influence of the outfall discharge on the flux of particulates to the bottom appeared to be greatest at or near the point of discharge and decreased rapidly within a distance of 2 to 3 km. Assuming a net current downcanyon of 5 cm/sec, this distance represents approximately 11 to 17 hours residence time in the water column for the settling wastewater particulates.

The organic content of the trapped solids decreases rapidly with distance from the discharge point (Figure 3). A line indicating the trend of the data has been fitted by eye. The shape of this curve is remarkably similar to that in Figure 2. The major influence of the discharged waste particulates, which average about 65% volatile solids, in determining the character of the particulate fallout was limited to an area within about 2 km of the discharge. If the effects of the waste particulates approach zero with increasing distance from the outfall, then the organic content of the collected particulates should approach that of natural marine fallout. We can estimate the probable range for the organic content of natural fallout to be 10 to 15% (Figure 3). Two samples collected with sediment traps placed in Catalina Canyon were analyzed for organic content according to the procedures already described. The values for the these were 11% and 12%, numbers which fit well with the hypothesis that most of the particulate matter collected by the sediment traps more than 2 km from the outfall is natural to the study area. Additional analyses of the chemical characteristics of the samples will be helpful in evaluating this interpretation of the data.

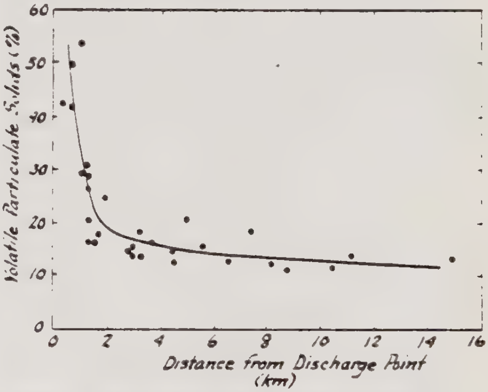

FIGURE 3. Organic content of settling particulates vs. location.

CONCLUSIONS

Although much of the data from this study are not yet available, the following preliminary conclusions have be made, based upon data presented in this paper.

1. Sediment traps are useful devices for the collection of settling particulate matter in the ocean.
2. Most of the waste particulates discharged at the head of Santa Monica Canyon fall to the bottom within a distance of 2 km of the point of discharge.
3. Natural fallout in the Santa Monica Canyon is in the range of 2 to 20 g/m²/day, with an organic content of 10 to 15%. High deposition rates occur aperiodically, primarily along the canyon axis; these probably result from resuspension and transport of the sediment by strong bottom currents.

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TRACE ELEMENT ANOMALIES IN MARINE ORGANISMS OFF SOUTHERN CALIFORNIA *

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ABSTRACT

Large quantities of DDT and trace metals are released annually to the coastal marine ecosystem off southern California via municipal wastewaters discharged through five major submarine outfall systems. Samples of the California seamussel, *Mytilus californianus*, and the Dover sole, *Microstomus pacificus*, were collected from throughout the Southern California Bight to determine if, around these local point sources, contamination of the nearshore biota had occurred. Highest DDT levels in seamussels were observed in specimens collected from the vicinity of a major outfall which, in the past, discharged effluents containing industrial wastes from the manufacture of this pesticide. Copper levels were significantly higher in urban seamussels than in either rural or island control specimens. In contrast, cadmium concentrations were significantly lower in the urban samples. Lead appears to be a wide spread contaminant of the southern California coastal region. Concentrations of chromium were highest in rural seamussels and silver concentration were highest in urban specimens. No significant differences in the nickel and zinc levels were observed between seamussels from any of the three regions. Similarly, no significant enhancements in the trace metal concentrations measured in Dover sole livers were observed despite the close association of the specimens with highly contaminated sediments.

INTRODUCTION

In recent years there has been increasing concern about pollution of coastal marine ecosystems. One aspect of this concern that has received considerable attention is the possibility that trace elements released to this environment through man's actions are being accumulated by organisms to unnatural levels that endanger both their health and their usefulness as seafood. Here we report results of studies into anomalous concentrations of 11 trace elements in two very different marine organisms, an intertidal mollusc, the California seamussel, *Mytilus californianus*, and a nearshore flatfish, the Dover sole, *Microstomus pacificus*, found off the densely populated coastal plain of southern California.

Approximately 11 million persons, or 5% of the Nation's population, inhabits the region between Point Conception and the U.S. Mexico border (Figure 1). Most of these people live in the Los Angeles/Orange County Basin * or near San Diego. The municipal wastewaters from these communities in large part are discharged from submarine outfalls a few kilometers offshore, generally at depths shallower than 100 m. Such discharges now total more than 1 billion gallons per day (approximately 1.4×10^{12} l/yr), comparable to the 1941–70 median annual flow of 1×10^{12} liters from surface runoff (United States Geological Survey, 1974). Approximately 95% of this municipal wastewater passes through five major treatment plants, where it generally undergoes only primary settling of solids

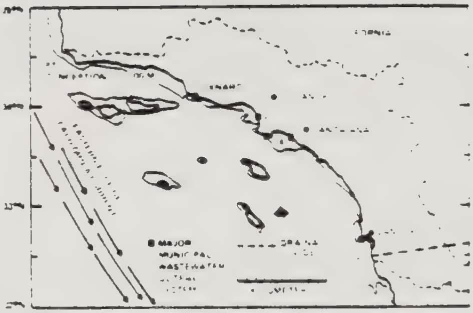

FIGURE 1 The Southern California Bight. Outfall systems are (1) Oxnard City, (2) Hyperion, Los Angeles City, (3) Joint Water Pollution Control Plant (JWPCP), Los Angeles County, (4) Orange County, and (5) San Diego City.

TABLE 1

Average trace element concentrations (mg/dry kg) in two types of particulates in the Bight *

Trace element	Percent associated with wastewater particulates	Wastewater particulates	Natural nearshore marine sediments
Silver	88	100	1.0
Cadmium	93	130	0.4
Chromium	94	1500	46
Copper	91	1600	16
Mercury	90†	4†	0.04
Nickel	58	350	14
Lead	94	610	8.5
Zinc	92	3000	63

* After Galloway, 1972a and Young et al., 1973.
† Estimates for Joint Water Pollution Control Plant (JWPCP) effluent only.

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* Contribution 39 of the Southern California Coastal Water Research Project

* Centered around the cities of Los Angeles and Santa Ana

before release (Southern California Coastal Water Research Project, 1973).

Young, Young, and Hlavka (1973) have summarized the importance of these wastewaters as sources of trace metals to the coastal ecosystem. For a number of metals, discharges from these systems contribute either a majority or a significant fraction of the estimated total input from the coastal plain. In collaboration with J. Galloway (University of California, San Diego), we found that most of these metals are associated with filterable particulates, and that the concentrations on such effluent solids are often two orders of magnitude above natural levels for bottom sediments found around the submarine outfalls (Table 1).

DDT AND TRACE METALS IN CALIFORNIA SEAMUSSELS

It has been shown that at least one chemical constituent of municipal wastewater can significantly contaminate the marine biota over a wide area. During summer 1971, we collected intertidal California seamussels, *M. californianus*, from coastal and island stations throughout the Southern California Bight. The whole soft tissues of specimens 4 to 6 cm in length were analyzed for chlorinated hydrocarbons by B. de Lappe and R. Risebrough at Bodega Marine Laboratory. Data on resultant DDT concentrations illustrate the striking effect one outfall system has had on residue levels of this pesticide in an intertidal invertebrate (Figure 2). Values decreased by factors of 50 to 100 in five directions away fromPalos Verdes Peninsula, the site of the outfalls of County Sanitation Districts of Los Angeles County. The source apparently was industrial DDT wastes released in very large quantities from a manufacturer of the pesticide over an undetermined period. During 1971, 20 metric tons of this waste were carried to the sea via effluent discharged from the Joint Water Pollution Control Plant, and we found 200 metric tons in the bottom sediments of the Palos Verdes shelf the following year (McDermott, Heesen, and Young, 1974).

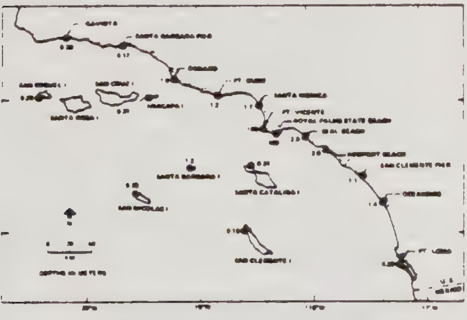

FIGURE 2. Total DDT concentrations (mg/dry kg) in whole soft tissues of California seamussel, *Mytilus californianus*, 1971. Average wet to dry weight ratio for these samples was 4.4 (Analyses by B. de Lappe and R. Risebrough).

To determine if there was corresponding widespread contamination of the nearshore biota from anthropogenic inputs of trace metals, digestive glands of seamussels obtained from the 1971 collection were analyzed by G. Alexander utilizing optical emission spectroscopy at the University of California, Los Angeles. Composites of this tissue from three male and three female specimens were measured, and application of the Wilcoxon signed-rank test revealed no significant effect of sex on the resultant metal concentrations.

The results do not indicate dramatic copper contamination of the intertidal zone off Los Angeles and Orange Counties (Figure 3), despite the fact that we estimate more than 500 metric tons of this metal were discharged during 1971 via municipal wastewaters from the three largest submarine outfall systems * of the bight. In contrast, analyses of trace metals in surface runoff conducted in collaboration with J. Morgan, California Institute of Technology, indicated that only about 14 metric tons of copper were carried into the marine environment by storm runoff from these two Counties. While large gradients were not observed, there is a suggestion of somewhat elevated values in mussels collected between Palos Verdes Peninsula and Newport Beach, and off Point Loma in San Diego.

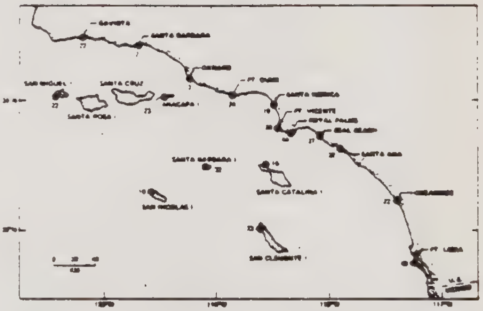

FIGURE 3. Copper concentrations (mg/dry kg) in digestive gland tissue of California seamussel, *Mytilus californianus*, 1971. Average wet to dry weight ratio for these samples was 3.8 (Analyses by G. Alexander).

Although these higher concentrations found off the major urban areas might be attributed to municipal wastewater inputs, we recently have reported another potentially important source of copper to the coastal ecosystem (Young, Heesen, McDermott, and Smokler, 1974). Approximately 200 metric tons of this metal in antifouling paints are applied annually to vessels in the Southern California Bight, with 120 metric tons being used at anchorages between Santa Monica and Newport Beach, and 50 metric tons being used at Mission and San Diego Bays near Point Loma. In contrast, San Diego municipal wastewater introduced only about 20 metric tons of copper off Point Loma during 1971. The highest copper concentrations (average: 68 ppm) found in the 1971 seamussel survey occurred on Point Loma between these two important San Diego anchorages, while the two next highest values (44 and 37 ppm) occurred to the north and south of San Pedro Harbor. Because the copper additives in antifouling paints are designed to effect marine invertebrates, such paints must be considered a candidate along with municipal wastewater as potential sources of the enhanced copper concentrations implied by the distribution found in *M. californianus.*

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* Hyperion Treatment Plant, City of Los Angeles: 340 mgd. JWPCP, County Sanitation District of Los Angeles County: 370 mgd. Orange County Sanitation District: 130 mgd.

In addition to municipal wastewater discharges and vessel-related activities, there are other potentially important anthropogenic sources of trace metals to the coastal zone, such as aerial fallout from atmospheric pollutants and direct industrial discharges. Although they have not been adequately quantified to date, the impact of these and other inputs associated principally with major population centers were assessed by evaluating any significant differences in concentration levels of potentially toxic trace elements in the 1971 intertidal mussels collected from three distinct population regions.

We utilized a statistical test developed by Tukey (1953) which allows for multiple comparisons between an unlimited number of groups. The one restriction is that there must be an equal number of sample points per group. Therefore, we separated the intertidal stations into three distinct population groups with five station values for each of the metals analyzed. The urban coastal group included Palos Verdes Peninsula, Santa Monica, Seal Beach, Newport Beach, and Point Loma. The Palos Verdes value was obtained by combining the concentrations from the Royal Palm and Pt. Vicente stations, which are located on the Peninsula near the JWPCP outfalls. The rural coastal group consisted of Gaviota, Santa Barbara, Oxnard, Point Dume, and Oceanside. Island control stations included San Miguel, Anacapa, San Nicolas, Santa Catalina, and San Clemente Islands. Santa Barbara Island was not included because the total DDT concentrations in mussels from this station were approximately five times that of the average for the other islands (Figure 2), suggesting an important influence of the JWPCP outfalls off Palos Verdes Peninsula.

TABLE 2

Average trace element concentrations (mg/dry kg) in digestive glands of the California seamussel, *Mytilus californianus*, showing significant regional differences * off southern California.

Trace element	Urban vs Island	Urban vs Rural	Rural vs Island
Silver	U > I (26) (10)	--	--
Cadmium	U < I (14) (21)	U < R (14) (26)	--
Chromium	--	U < R (5) (15)	R > I (15) (2)
Copper	U > I (38) (20)	U > R (38) (22)	--
Nickel	--	--	--
Lead	U > I (18) (6)	--	R > I (21) (6)
Zinc	--		--

* 95% Confidence limit.

The results of the analysis for the seven trace metals considered show that relatively constant values of about 20 mg/dry kg (ppm) lead were observed in both the urban and rural coastal zones, and that this level was significantly higher than the island mean of 6 ppm (Table 2). Only those differences between digestive gland concentrations which are statistically significant at the 95 percent confidence level are listed. This distribution may be a result, in part, of the large quantity (approximately 7000 tons) of tetraethyl lead burned annually in internal combustion engines and introduced via automotive exhaust to the coastal plain (Huntzicker, Friedlander, and Davidson, 1975).

Of the remaining six metals, the mean urban copper concentration (38 ppm) was significantly higher than both the rural and island means (22 and 20 ppm, respectively). For silver the urban mean (26 ppm) was significantly higher than the island mean (10 ppm), but not the rural mean (12 ppm). In the case of cadium, the urban mean (14 ppm) was significantly lower than both the rural and island means (26 and 21 ppm, respectively). For chromium, the rural mean (15 ppm) was significantly higher than both the urban and island means (5 and 2 ppm, respectively). In the case of nickel and zinc, no significant differences between groups were observed; bight-wide averages for these two metals were 8 and 76 ppm, respectively.

Although individual results for these seven potential pollutants are quite varied, a general conclusion which may be drawn from this comparison is that there does not appear to be a pattern of dramatic urban enhancements of the trace metals analyzed in this intertidal invertebrate. Urban depressions as well as enhancements are observed, and regional group means generally agree within a factor of two or three. The biological implications of such variations are not yet well understood.

TRACE METALS IN DOVER SOLE

Following this regional survey, we conducted an intensive investigation into trace element

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DEVELOPMENT AND USE OF SONAR MAPPING FOR PELAGIC STOCK ASSESSMENT IN THE CALIFORNIA CURRENT AREA[1]

Roger P. Hewitt, Paul E. Smith, and John C. Brown[2]

ABSTRACT

A method for pelagic fish stock assessment is presented which utilizes a fixed sonar beam for mapping fish schools. Samples of the two major acoustic properties of fish schools are presented, i.e., acoustically derived horizontal dimensions (representative of school volume) and target strengths (which may be representative of school compaction). Sampling biases and sources of sampling variability in the measurement of these properties are discussed. The results of two experiments, conducted to determine the weight of a fish school as a function of its acoustic characteristics, are presented. In the first experiment, an acoustically transparent trap was used to recreate an aggregation of fish and in the second, commercial fishing boats were chartered to capture whole schools. An automated sonar data acquisition and processing system is described and test results presented. The results of paired automated surveys of the Los Angeles (southern California) Bight are presented and discussed. The paper reports development of the sonar-fish school mapping method first documented by P. E. Smith in 1970.

Field investigations, conducted in cooperation with the Navy and the California Department of Fish and Game, indicate a median school size of 30 m diameter, a mean fish density of 15 kg of fish biomass per square meter of horizontal school area, and a biomass estimate of 1.23 to 2.30 × 10^6 metric tons for pelagic schooled targets in the Los Angeles Bight.

Fishermen have used hydroacoustic apparatus for locating concentrations of fish for almost as long as practical echo sounding devices have been available, although quantification of the information they provide has been attempted only in recent years. Horizontal echo ranging (sonar) to locate fish schools was first used off the coast of California in 1946 (Smith 1947; Smith and Ahlstrom 1948). The 1950 progress report of the California Cooperative Sardine Research program notes the use of sonar and echo sounders on the RV *Yellowfin* for locating fish schools, and cites the "considerable experimental value" of the acoustic apparatus. A research sonar on the RV *David Starr Jordan* has been used to count fish schools in the eastern tropical Pacific (McClendon 1968) and in the California Current area (Smith 1970). For recent reviews of the use of echo sounders and sonars for fishery research, consult Forbes and Nakken (1972) and Cushing (1973).

The work presented here is a method for quantifying sonar records and further using these records for estimating the size of pelagic fish stocks. The paper is divided into four sections:

1. The section entitled "Sources of sampling variability" describes the scale and variance of measured acoustic parameters of fish schools, i.e., horizontal fish school dimensions and peak target strength or echo intensity. It further discusses major biases affecting the measurement of these values.
2. The estimation of fish biomass in an aggregation involves the determination of a conversion factor by which the detected horizontal area of a fish school may be multiplied. Experiments to determine the weight of the fish under a square meter of school area are described in a section entitled "Horizontal school area to biomass conversion factors."
3. An automated data acquisition system is described in the third section.
4. The results of a paired sonar survey of the Los Angeles Bight, utilizing the automated system and a biomass factor determined during the cruise, are presented and discussed in the fourth section.

This report is the second in a series describing

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[1] Conducted under a grant from the Marine Research Committee of the California Department of Fish and Game as part of the California Cooperative Oceanic Fisheries Investigations, and in cooperation with the United States Navy.

[2] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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FISHERY BULLETIN: VOL. 74, NO. 2, 1976.

progress on a number of objectives established in early 1968. In order to develop "sonar mapping" as a stock assessment tool, it was decided that such a system should be able to: 1) count the number of schools per unit area in the upper mixed layer from a ship proceeding at 12 knots, 2) measure the horizontal size of each fish school, 3) calculate the biomass of each school, 4) estimate the size of individual fish within a school, and 5) distinguish the northern anchovy from all other schooling species.

Smith (1970) developed a technique for "mapping" fish schools in the area where the northern anchovy, *Engraulis mordax*, is abundant off the coast of southern California. Sonar mapping differs from echo sounding; with sonar, estimates can be made of the number of fish schools per unit area, of their horizontal dimensions, and of the degree of aggregation of fish schools. We do not routinely estimate depth of the school in the water column, nor thickness of the school in the vertical plane. Hull-mounted echo sounders provide estimates of the number of schools per line transect deeper than 4 m, measures of chords across the horizontal dimension of the school in the plane of ship travel, depth in the water column, and thickness or vertical height of the fish school. Experience indicates that the process of "sonar mapping" encounters one or two orders of magnitude more fish-school targets per unit of ship time as compared to echo sounding from the same vessel. It is important to emphasize that this technique was developed because fish schools are frequently found in the upper mixed layer of the ocean where echo sounders are relatively ineffectual at counting or measuring them.

In the first report on this project, Smith (1970) described a series of experiments designed to determine the feasibility of the use of sonar to count and measure the size of pelagic fish aggregations (objectives 1 and 2). Optimum instrument settings were determined for source level, receiver gain, pulse length, transducer bearing, transducer directivity, and range. Methods were developed for correcting target width (dimension measured on axis parallel to ship's track) for the effect of the beam angle and for correcting target count "edge biases." Since no target was counted unless it lay entirely within a specified range, the latter adjustment was made to compensate for the narrowing possible interval of detection for larger targets.

Holliday (1972, 1974) investigated the frequency domain processing of fish school echoes using experimental equipment brought aboard the *David Starr Jordan*. By detecting and measuring Doppler spread, Holliday was able to calculate tail beat amplitudes of schooled fish and, indirectly, their length (objective 4).

Holliday also examined the resonance structure of pulse returns from fish schools and was able to detect the presence or absence of a swim bladder in the school constituents. This information, when supplemented by observations on school behavior and free vehicle camera drops, may be used to distinguish anchovy from other pelagic schooling organisms in a sample taken randomly from targets encountered during a survey (objective 5). The statistical base thus obtained would be applied to the entire survey.

The California Department of Fish and Game (CF&G) has been engaged in sea surveys using sonar methods since 1967 (Mais 1974). Its approach has been the collection of large amounts of data and its interpretation, while the work at the Southwest Fisheries Center (SWFC) has been in the isolation of sampling errors and the development of an automated hydroacoustic data acquisition and processing system. As such, the two groups complement each other with field experience and technological development.

SOURCES OF SAMPLING VARIABILITY

We have made the assumption that quantitative errors associated with system instrumentation are small in comparison to errors generated by sampling an adult schooling population whose behavior is little understood. For this reason, we monitored our sonar system response when it was operated in a variety of circumstances and changed that system in answer to practical rather than theoretical considerations. Using operating techniques developed in 1968, school size frequency distributions were generated and a lower detectable size threshold defined; school target strengths were calculated and compared with similar work conducted by the Navy and the CF&G; the relationship between the detected occurrence of pelagic fish schools and bottom topography was investigated; and the variable range of detection of schools due to internal waves was studied (Smith[3]).

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[3] Smith, P. E. 1973. The effects of internal waves on fish school

Based on Smith's (1970) work, sonar mapping cruises aboard the *David Starr Jordan* were conducted with a 30-kHz sonar unit directed 90° to starboard and 3° down. The sampled range band was 200 to 450 m from the transducer. The receivers were rebuilt using solid state circuitry with the remaining system as described by Smith (SIMRAD 580-10 Scientific Sonar and Sounder).[4]

Target Size

Frequency distributions of fish school sizes were generated from data taken on several cruises (April-May, November, December 1973; and March-April 1974) using the maximum difference between the leading and trailing edge of the echo envelope, corrected for pulse length, on an axis perpendicular to the ship's track. The calculation of target widths (measured on an axis parallel to the ship's track) was discontinued due to uncertainties in choosing the effective beam width (see Smith 1970), fluctuations in the ship's speed, and the inability to quantify other factors which may affect apparent target width (i.e., target strength).

School size distributions (based on range differences) remained nearly constant during several sampling periods and agreed well with a much larger sample collected by the CF&G. A total of 4,355 sonar targets were counted and assigned to size classes on three cruises approximately 6 mo apart. Ten-meter class intervals were used and frequencies were corrected for recording edge bias employing the method described by Smith (1970). This bias is encountered when one excludes targets which do not entirely occur within the observation band. Thus, frequencies of targets other than point sources, are underestimated by virtue of the fact that their physical size limits the probability of their detection. To determine unbiased relative proportions of target sizes, one must correct observed target count (those targets which lie entirely within the observation band) to a count of targets whose centers lie within the observation band.[5]

In developing a correction for recording edge bias, a diagram may be useful. In Figure 1 a school of diameter d is shown at the maximum and minimum ranges of detection for an observer on a ship sampling an observation band of k units. The difference between the maximum and minimum range of detection is $k - d$ units.

Let A represent the event that a school of d diameter has its center within an observation band of k units. Let B represent the event that a school of d diameter is not intersected by either edge of the observation band. Then the probability of event B occurring given that event A has occurred may be expressed:

$$P[B/A] = \frac{k-d}{k}.$$

Further, let N_d represent the count of targets of diameter d who lie entirely within the observation band. Let N'_d represent the count of targets of diameter d whose centers lie within the observation band. Since N'_d represents both edge intersected and non-edge intersected targets of diameter d, the portion of non-edge intersected targets may be estimated by:

$$N_d = N'_d P[B/A] = N'_d\left(\frac{k-d}{k}\right).$$

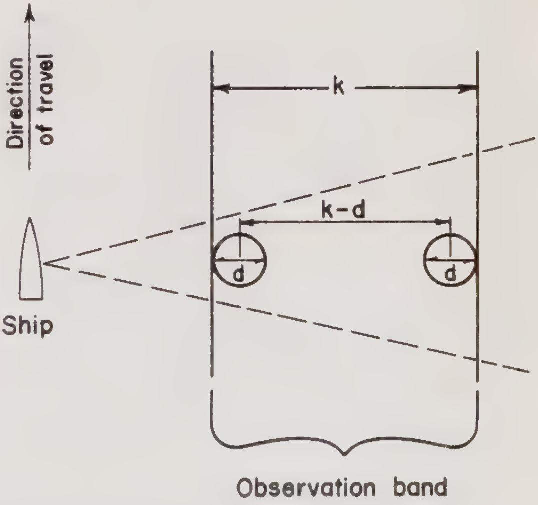

FIGURE 1.—Plan view of sonar mapping technique showing maximum and minimum ranges of detection for a target of diameter d within an observation band of k units.

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mapping. Presented at the ICES-ICNAF-FAO Symposium on the Acoustic Methods in Fisheries Research, Bergen, Norway, Contrib. No. 8, 13 p.

[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5] It is assumed that range-dependent, size-specific target losses are a minimum for the observation band sampled (Smith 1970). A similar study expanded to include the effects of target strength on detection ranges would be of value.

In actual practice N_d is tabulated. N'_d is then estimated by rearranging the above expression:

$$N'_d = N_d\left(\frac{k}{k-d}\right)$$

where N_d = observed class frequency
N'_d = edge corrected class frequency
k = extent of the observation window in meters (usually 250 m)
d = mean class diameter in meters.

As an example, when using a 250-m observation band, a 50-m target may be entirely detected over 200 m of that band, whereas a 100-m target must occur within a band of only 150 m to be detected. If one counts 10 50-m targets and 3 100-m targets, the counts, when corrected for edge bias, will be 10(250)/(250 − 50) = 12.5 and 3(250)/(250 − 100) = 5, respectively.

Horizontal school area is calculated by multiplying N' by the area of a circle whose diameter is equal to the class mark. The calculation is based on the assumption that with an increasing sample size the school dimension perpendicular to the ship's track will approximate the diameter of a circle whose area is equal to the area of a given school, however irregularly shaped. This assumption contains the condition that the orientation of a sample of schools is random and in no way related to that of the survey ship.

The resulting cumulative frequency diagram (Figure 2) would indicate that over 50% of the schools are less than 30 m in diameter while 90% of the horizontal school area is contributed by schools larger than 30 m in diameter. Mais' (1974) experience with over 23,000 schools (corrected for edge bias) in the same survey area indicated a similar distribution with a mode at 30 to 40 m (Figures 2, 3).

Smaller schools (<20 m in diameter) were likely to be undersampled by both the National Marine Fisheries Service (NMFS) and CF&G as the probability of their detection decreases faster with range than larger schools. Even if an exponential model of target size obtains in nature, schools smaller than 20 m would contribute little in amounts of horizontal school area.

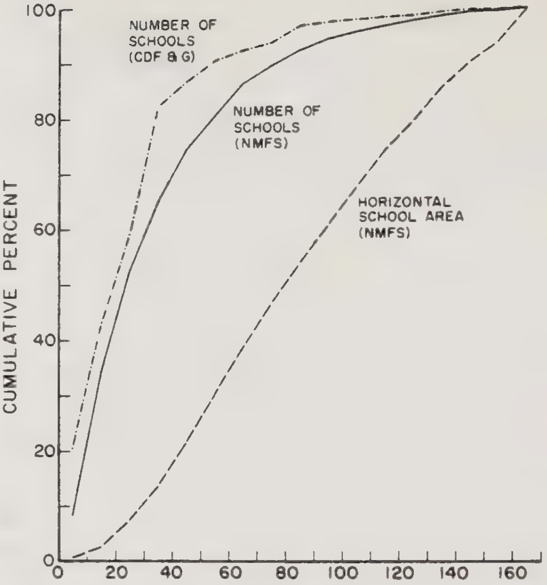

FIGURE 2.—Cumulative frequencies of sonar-detected fish schools by size and their contributing horizontal area (NMFS data only). The two modes in the CF&G data curve, drawn from a much larger sample (5×), might suggest either a systematic sampling error or optimum fish school sizes.

The significance of a negative bias in the lower end of the observed school size distribution may be evaluated by fitting a power curve to that portion of the distribution between 15 and 165 m. The equation, derived by a least squares fit, assumes the following form:

$$y = ax^b.$$

Using the NMFS sample of 4,355 targets:

$$N'_i = 428{,}864\ (D_m)_i^{-1.874}$$

where N'_i = edge-bias corrected target frequency within class i
$(D_m)_i$ = mean diameter of class i in meters.

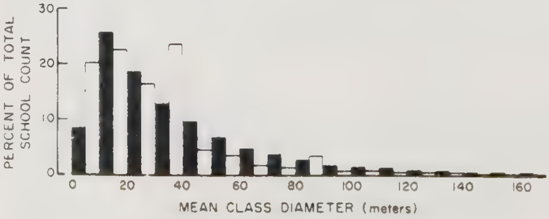

FIGURE 3.—Percent of total school count by size class. NMFS data are represented by the shaded bars; the open bars are calculated from CF&G data.

The correlation coefficient (r) = −0.969. Table 1 summarizes horizontal school area contributions by size class for observed frequencies corrected for edge bias and for frequencies derived from the exponential model. In both cases more than 90% of the area was contributed by schools larger than 20 m. The importance of horizontal school area is that it is probably proportional to the tonnage of fish in schools and, in this sense, decreases the significance of any bias in the counts of small schools.

TABLE 1.—Cumulative percent of total horizontal school area contributed by size class for observed frequencies (corrected for edge bias) and for frequencies derived from an exponential model.

Mean class diameter	N	N'	Model	Cumulative % A	
				Observed	Model
5	420	429	21018	0.09	4.24
15	1,247	1,347	2682	2.48	9.12
25	843	937	1030	7.17	14.32
35	556	647	548	13.52	19.73
45	403	491	342	21.50	25.32
55	277	355	235	30.11	31.05
65	182	246	172	38.44	36.91
75	124	177	131	46.33	42.88
85	86	130	104	53.98	48.98
95	57	92	84	60.63	55.09
105	47	81	70	67.79	61.39
115	32	59	59	74.07	67.72
125	22	44	50	79.58	74.03
135	19	41	44	85.61	80.42
145	11	26	38	90.02	86.89
155	7	18	34	93.57	93.53
165	10	29	30	99.99	99.99
>165	12				
	4,355				

Diurnal and Seasonal Effects

Time specific frequency distributions were drawn for data collected on cruises in April-May and in November 1973 for the purpose of discerning variations in sizes and detection of schools during various times of the day. While variations were noticed, their pattern was neither pronounced nor consistent from cruise to cruise. This is not to say that daily changes in schooling behavior do not exist, but that our data base is insufficient, at present, to delineate them. In the evening, discrete, well-formed schools of anchovy have been observed to disperse into a thin scattered layer but no program of study on this problem has been undertaken.

The data base is insufficient to detail seasonal changes in school size distributions, although, from communication with Mais and several commercial fishermen, we have reason to expect somewhat larger schools in the fall and smaller, scattered schools in the spring. Mid-spring is considered to be the main spawning season of the northern anchovy.

Target Strength

Acoustic target strength is proportional to the ability of an object or group of objects to reflect sound waves. Acoustic reflections from schools of fish are not presently well enough understood for rigorous characterization of the biomass of a fish school by the use of sonar. Nevertheless, we have measured apparent fish school target strengths with the objective of providing data which may lead to the quantification of fish schools in terms of total biomass.

Peak echo amplitudes were collected and corrected for propagation and absorption losses by employing the active sonar equation:

$$EL = SL - 2TL + TS$$

where EL = echo level in decibels (dB)
SL = source level in decibels, reference 1 μbar at 1 m
TL = transmission loss in decibels
TS = target strength in decibels.

Solving for target strength and using signal voltage level as a measure of echo level:

$$TS = 20 \log V - k + 40 \log R + 2 \propto R$$

where V = peak echo signal amplitude in volts
k = calibration coefficient which is the algebraic sum of source level, receiver sensitivity, and system gain expressed in decibels
$40 \log R + 2 \propto R$ = range dependent transmission loss (assuming spherical losses as in a homogeneous fluid) where R = midrange of target (as an approximation of the (location of peak echo amplitude), and $\propto$ = absorption coefficient expressed in decibels per meter.

Figure 4 illustrates five samples of peak target strengths computed from data taken by the

NMFS, U.S. Navy, and CF&G. Two of the distributions are "absolute" target strength in decibels and three are relative measurements, i.e., the calibration coefficient was not included in the calculations. The range of peak target strengths observed in any one sample varies from 28 to 34 dB. The two distributions of absolute target strength were obtained with the same sonar unit aboard the *David Starr Jordan*. The value of the calibration coefficient was recomputed after hydrophone calibration between cruises and remained constant. As such, the favorable comparison between the samples may be deceptive. The CF&G data were obtained and processed in a similar fashion using a 38-kHz sounder.

The theoretical target strength of a fish school has been discussed by Weston (1967) and Uretsky (1963). Modeling a fish school as a two dimensional array of bubbles in a liquid, both Weston and Uretsky predicted a sharp drop in response

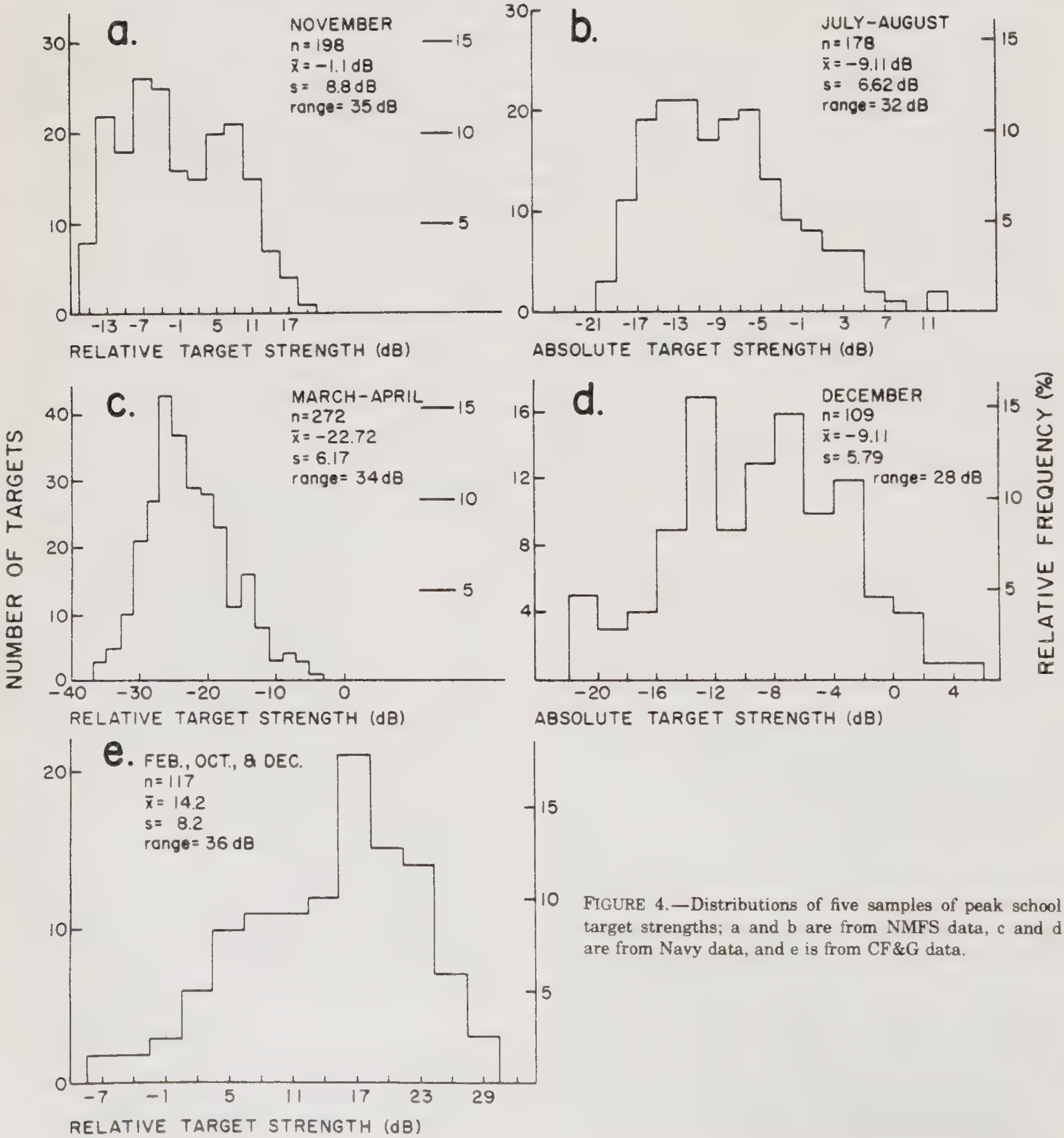

FIGURE 4.—Distributions of five samples of peak school target strengths; a and b are from NMFS data, c and d are from Navy data, and e is from CF&G data.

with increasing frequency above resonance. Using this approach, the energy scattered by the boundary of a fish school ensonified (irradiated acoustically) with 30 kHz sound becomes negligible.

Weston (1967) further suggested that an incoherent addition of reflected energy from individual fish may be expected as sound is transmitted across the boundary of a fish school. At 30 kHz, this component of target response becomes dominant and is reduced (or enhanced) by multiple scattering and absorption within the school.

The target response due to sound scattering by individual fish, assuming a mean wave phase interference of zero, may be calculated by summing the scattering cross sections of the fish comprising the target. Expressed in target strength, TS:

$$TS = TS_i + 10 \log n \text{ (decibels)}$$

where TS_i = the average target strength of the individual scatterer

n = the number of scatterers contributing to the total echo.

The number of scatterers contributing to the measured echo, n, may be estimated by applying observed and theoretical school densities (fish per cubic meter) to the ensonified volume. The ensonified volume may be estimated from:

$$V = \frac{c\tau}{2}(d)(D) \text{ (cubic meters)} \qquad (1)$$

where $\frac{c\tau}{2}$ = the range extent of the volume sampled by a sound pulse τ seconds long and moving at a speed of c meters per second

D = the vertical dimension of the school in meters

d = the horizontal dimension of the school.

School dimensions, D and d, are further limited by beam geometry, i.e., a school may not be fully ensonified if its dimensions exceed the effective beam width at the range of detection. The effective horizontal beam width may be estimated as that between the half-power points or:

$$2R \tan \beta$$

where R = range of detection

$\beta = 5°$ for the 30-kHz transducer used in this study.

Thus, d is the smaller of the measured horizontal dimensions or $0.175R$. Vertical dimensions of fish schools are not readily measured with sonar. However, in studying echograms of thousands of schools, Mais (1974) noted less variation in the vertical school dimension than the horizontal dimension and reported a mean school thickness of 12 m. The vertical effective beam width is estimated to be 12° or 42 m at 200-m range. If D is then assumed to be 12 m for all schools, there is no limitation imposed by the vertical beam width except that caused by vertical positioning of the school.

Using a 10 ms pulse length and estimating the speed of sound in a seawater medium at 1,500 m/s, Equation (1) becomes:

$$V = 90\, d$$

where d is the smaller of the measured horizontal dimensions or $0.175\, R$.

Mais (1974) reported visual observations of anchovy schools and estimated average packing density at 50 to 75 fish/m^3. Graves[6] analyzed in situ photographs of three anchovy schools and reported a mean density of 115 fish/m^3 at a mean spacing of 1.2 body lengths. Hewitt[7] used an idealized model of anchovy school compaction and calculated school densities of 0.5, 1.4, 6.6, 217, and 4,219 fish/m^3 at interfish distances of 10, 7, 4, 1, and 0.2 body lengths, respectively.

The target strength of an individual scatterer, TS_i may be estimated from considerations of acoustic theory and extensions of empirical measurements. Weston (1967) had shown the acoustic response of an ideal gas bubble to be essentially independent of frequency above resonance and proportional to the surface area of the bubble. When predicting the response of a fish swim bladder, Weston suggested an enhancement of

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[6] Graves, J. 1974. A method for measuring the spacing and density of pelagic fish schools at sea. SWFC Administrative Report No. LJ-74-44. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[7] Hewitt, R. 1975. Sonar mapping in the California Current area: A review of recent developments. Unpubl. manuscr. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038. The compaction model cited here used an anchovy of 12 cm standard length and computed the space required for the fish and a surrounding volume expressed in body lengths. The inverse of the resulting volume yields compaction in fish per cubic meter for a school of fish uniformly distributed in space.

75% due to shape distortion. Expressed in target strength:

$$TS_i = 20 \log L - 25 \text{ (decibels)} \qquad (2)$$

where L is the fish length in meters. Swim bladder volume is assumed to be 4.1% of total fish volume and the radius of a sphere of equal volume equal to $0.043\, L$ (after Haslett 1965).

Using a standard length of 12 cm as typical of anchovy school constituents detected by sonar (Mais 1974), Equation (2) yields a TS_i of −43.4 dB. It should be noted that Equation (2) makes no provision for reflection, interference, or attenuation of sound waves by fish tissue.[8]

McCartney and Stubbs (1970) measured maximum dorsal aspect target strengths of six fish species at varying frequencies and lengths. They fit Equation (3) to their data and further showed that the swim bladder can account for practically all of the scattering over a wide band of frequencies:

$$TS_i = 24.5 \log L - 4.5 \log \lambda - 26.4 \qquad (3)$$

where λ = the wavelength of incident sound defined as $c(f)^{-1}$, where c is the speed of sound in a saltwater medium $\approx$ 1,500 m/s^{-1} and f is the frequency. For a 12 cm anchovy ensonified with 30 kHz sound, Equation (3) gives a TS_i of −43.1 dB.

Love (1971) reviewed maximum dorsal and side aspect target strength measurements made by several investigators. The data were obtained using fish from eight different generic orders, varying 100-fold in length, some with swim bladders and some without, and ensonified over a frequency range of 8 to 1,480 kHz. For dorsal aspect, Love related maximum target strength, fish length, and frequency by:

$$TS_i = 19.4 \log L + 0.6 \log \lambda - 24.9. \qquad (4)$$

For the anchovy described above, Equation (4) predicts a TS_i of −43.5 dB at dorsal aspect.

Love described the side aspect data with the following equation:

$$TS_i = 22.8 \log L - 2.8 \log \lambda - 22.9 \qquad (5)$$

or −40.2 dB for the anchovy described at side aspect.

A similar regression on target strength measurements taken from dead fish in dorsal aspect by six investigators and collated by Haslett (1965) would describe a TS_i of −49.8 dB for a 12-cm fish ensonified at 30 kHz (McCartney and Stubbs 1970). An application of the equations that Shibata (1970) used to describe his results yielded values of −42.8 dB for maximum dorsal aspect target strength and −40.0 dB for maximum side aspect target strength.

Several authors have noted that acoustic equipment commonly used by the biologist operates at frequencies (10 to 200 kHz) which generate sound at wavelengths comparable with the size of fish under study. Interferences will occur among the scattering components of a fish (swim bladder, flesh, skeleton, and organs) and may be expected to be a function of species and aspect. Further, our measurements are of peak school target strength taken from several transmissions along one tangential to the school and may not be the maximum value which would be obtained from interrogation at several angles.

Let us return now to the original calculations, i.e., the incoherent summation of echoes from an aggregation of fish which may now be expressed as:

$$TS = TS_i + 10 \log \left[q\ (90\ d)\right] \qquad (6)$$

where TS_i may vary from −50 to −40 dB, q is the school density in fish per cubic meter and may vary from 0.5 to 4,219, and d may vary from 5 m (mean diameter of the minimum class size) to 79 m (0.175 R at R = 450 m, the maximum range within the observation band). The expected range of peak school target strengths (assuming incoherent addition and no interference or absorption within the school) are listed below for four assumptions of fish target strength, TS_i:

TS_i	*Minimum* TS where q = 0.5 fish/m^3 and d = 5m	*Maximum* TS where q = 4,219 fish/m^3 and d = 79 m
−40 dB	−16 dB	+35 dB
−43 dB	−19 dB	+32 dB
−45 dB	−21 dB	+30 dB
−50 dB	−26 dB	+25 dB

where τ = 10 ms, β = 5°, and D = 12 m.

Based on a framework of several assumptions, we may expect a range of peak school target strengths of about 50 dB whose position on the decibel scale is determined from the value one assumes to be the average target strength of the individual scatterers comprising the school.

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[8] Holliday (1972) reported an average swim bladder volume of 2.8% of the total fish volume for a sample of 239 anchovy. The use of this value predicts an anchovy swim bladder response of −44.3 dB.

From the data presented so far (Figures 3, 4) we may assume the most probable target strength for all schools to be −9 dB. Further, assuming that the "typical" school has a vertical dimension of 12 m and that the measured target strength is the summation of scattering strength of the individual fish ensonified with no effects from multiple scattering or attenuation, we may use Equation (6) to estimate q:

TS_i	q	*Spacing*
−40 dB	0.93 fish/m^3	8.1 body lengths
−43 dB	1.86	6.5
−45 dB	2.95	5.5
−50 dB	9.33	3.4

Bottom Topography

Fixed transect surveys require that the distribution of schools be independent of fixed geographic locales whose scale is smaller than transect spacing.

A cruise in March-April 1974, was designed to test a postulated relationship between the occurrence of pelagic fish schools and bottom topography. The area chosen was the Los Angeles Bight and for the purposes of the experiment was defined as that body of water bounded by the southern California coast from Pt. Arguello to the U.S.-Mexican border and seaward by a line extending south from Pt. Arguello to a point west of San Miguel Island, thence southeast along an extension of the Santa Rosa-Cortez Ridge to a point north of the east end of Cortez Bank, thence east to the intersection of the shoreline and the U.S.-Mexican border. The survey area, excluding island masses, contains approximately 11.5×10^3 square nautical miles of sea surface area.

The "Bight" was further divided into four classes of bottom topography and transects designed to distribute survey effort within these zones as described below. The method used was to delineate and compute the combined areas of the first three categories and then assign the remaining area to the fourth general zone.

Bottom topography	*Total area (nautical miles^2)*	*% of survey area*	*% of sampling effort*
Banks and seamounts	547	4.8	14.4
Basins and troughs	2,946	25.9	27.4
Escarpments and canyons	467	4.1	24.1
Slopes	7,510	65.2	34.1

Combined seas and swells in excess of 7 feet prohibited sonar operations on 1 day out of 12 and somewhat altered the distribution of survey effort. A detailed breakdown of zones and actual survey effort is listed in Appendix Table 1.

Daylight sonar tracking was accomplished during two time periods separated by 2 wk: 25-29 March, 1 April, and 15-19 April 1974. No difference in schooling behavior was detected between the two periods and results are presented for the total cruise time in Appendix Table 2. If an area was surveyed and no targets were detected, a "0" under "No. targets obs." so indicates; if an area was not surveyed during one or both time periods then no numbers are recorded in the appropriate columns. "Linear nautical miles surveyed" is the distance traversed while sonar tracking over the designated area. The observation window (250 m wide beginning at 200 m from the ship, and 90° to starboard from the ship's track) is multiplied by the linear distance traversed and divided into the number of targets observed to obtain target density, expressed in units of targets per square nautical mile.

The geographic names of various topographic features are commonly accepted and can be located on National Ocean Survey bathymetric maps (numbers 1205N-15, 1206N-16, 1306N-19, and 1306N-20) with the exception of the following features informally named for the sake of convenience: Coronado Bank (lying immediately to the east of Coronado Escarpment), San Diego Escarpment (along the west side of the San Diego trough), Cortez Escarpment (east-northeast of Cortez Bank), San Clemente Bank (a relatively deep bank northeast of San Clemente Island), Santa Rosa North and South Bank, San Nicolas Escarpment (southeast of San Nicholas Island), Santa Cruz Bank (south-southeast of Santa Rosa Island), Santa Barbara Escarpment (west of Santa Barbara Island at the southeast end of Santa Cruz Basin), Santa Barbara Bank (north of Santa Barbara Island), and Santa Monica Escarpment (along the southwest side of Santa Monica Basin).

The data fail to support the notion that the occurrence of pelagic fish schools can be related to bottom topography over which they are detected. Mean target densities (number of targets observed per square nautical mile) were calculated for the four classes of bottom topography and although these densities range from 2.98 (banks and seamounts) to 8.23 (escarpments and can-

TABLE 2.—A comparison of the variance in detected target densities within the classes of bottom topography (zone) and between the zones. Probability <0.5 that there is an other than random relationship between the four classes of bottom topography and detected school occurrence rates (target densities).

	Targets observed (no.)			Target density (targets/nmi^2)		
Zone	25 Mar.- 1 Apr.	15-19 Apr.	Total	25 Mar.- 1 Apr.	15-19 Apr.	Total
Banks and seamounts	36	2	38	3.57	0.75	2.98
Basins and troughs	117	244	361	4.42	12.08	7.74
Escarpments and canyons	29	229	258	2.11	12.81	8.23
Slopes	194	69	263	8.55	3.25	5.98

	Sum of squares	Degrees of freedom	Means of squares	*F*
Within zone	72.9765	29	2.5164	
Between zones	2.9932	3	0.9977	0.40

yons), an analysis of the variance would suggest that there is no variance between the zones that could not be explained by the existing variability within the zones (Table 2).

HORIZONTAL SCHOOL AREA TO BIOMASS CONVERSION FACTORS

Fish Trap Experiment

The first effort toward determining a horizontal school area to biomass conversion factor was conducted in 1970 and briefly described in the discussion following the presentation of Smith's (1970) paper and transcribed in the publication of that paper.

An acoustically transparent trap (Figure 5) was constructed and live northern anchovy enclosed. Two groups of fish were ensonified and their horizontal area measured. A 354-kg group yielded a target strength within the range frequently encountered while a 2,017-kg group's target strength was well above that observed in nature for schooling fish.

Ensonification of additional weight groups was not possible due to the presence of predators and attempts at visual observation of the fish aggregation using a manned submersible eventually destroyed the trap. A value of 31 kg of fish biomass/m^2 was derived from the 354-kg group and judged to be our best estimate (Table 3). Mais (pers. commun.) reports from his experience

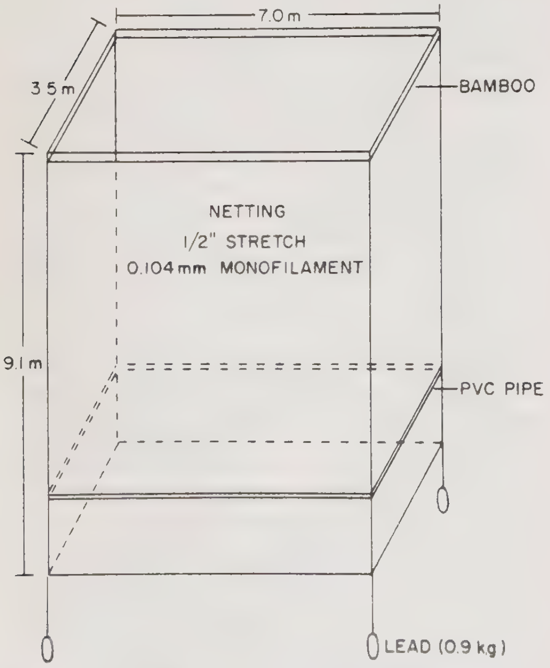

FIGURE 5.—Diagram of an acoustically transparent trap for ensonifying a group of fish of known size and weight.

TABLE 3.—Computation of a horizontal school area to biomass conversion factor from data gathered during the fish trap experiment (February 1970).

	50-fish sample		354-kg group		2,017-kg group	
Weight class (g)	No. of fish	% of sample weight	No. of fish	Total weight (g)	No. of fish	Total weight (g)
10	24	33.8	11,925	119,652	68,175	681,746
15	15	31.7	7,481	112,218	42,626	639,389
20	9	25.4	4,496	89,916	25,616	512,318
25	1	3.5	496	12,390	2,824	70,595
30	0	0	0	0	0	0
35	0	0	0	0	0	0
40	1	5.6	496	19,824	2,824	112,952
Total	50	100.0	24,894	354,000	142,065	2,017,000

	354-kg group		2,017-kg group	
Surface area[1]	[2]Mt/m^2	No./m^2	Mt/m^2	No./m^2
11.39	0.031	2,190	0.177	12,473

[1] The fish are schooled in an ellipse with a major radius of 2.90 m and a minor radius of 1.25 m (surface area 11.39 m^2).

[2] Metric tons per square meter.

a representative anchovy school compaction around 50 fish/m^3 or a distance of two body lengths between fish. Using a single fish weight of 18 g and an average school thickness of 12 m (Mais 1974), one obtains a horizontal school area to biomass conversion factor of 8.4 kg/m^2.

Charter Boat Experiment

A second experiment was designed and executed in late summer 1974, to relate measured school size, calculated target strength, and school compaction. Purse seine boats were chartered to make directed sets on fish schools first ensonified by the acoustic system aboard the *David Starr Jordan*.[9] Target strength and school size were calculated from the observation. The fishing boat supplied information on the tonnage caught and the portion of the school taken. Using these data, a biomass conversion factor was calculated for each school by dividing the total estimated school tonnage by a circular area based on the difference between its near and far ranges.

Fifty-two sets were judged to be the minimum sample size necessary to distinguish between two estimates of the portion of detectable pelagic aggregations that are schools of northern anchovy. Squire (1972), using data from 6 yr of observations from several commercial air spotters, reported that at least 50% of the surface schools off southern California can be expected to be anchovy. Mais (pers. commun.) estimates that 90% of the schools sampled by mid-water trawl are anchovy.

Seventy-six sets were made landing 1,901 short tons of anchovy; 63 were directed by the *David Starr Jordan* and 13 directed by the State of California's RV *Alaska*. Forty-nine positive data points were tabulated from the *David Starr Jordan*'s work and eight from the *Alaska*.

Average target size was 119 m (as measured by the difference between the near and far ranges on a line perpendicular to the ship's head) with a range from 31 to 305 m. Average peak target strength was +5.18 dB (as calculated from peak amplitude and range dependent losses) with a range from −9 to +18 dB and a SD of 5.63 dB.

Practical considerations forced us to expend a larger portion of effort on schools of larger than average size and target strength. This circumstance accounts for the fourfold increase in median target size and a 15-dB increase in mean target strength over a sonar-generated data base reported earlier. In addition, this sample was chosen from a detected school population whose acoustic dimensions were, in general, larger than that experienced on previous cruises.

To facilitate the direction of sets, the observation window was increased from 250 to 500 m wide and moved 100 m closer to the vessel. A time-varied gain increase was also accomplished in the receiver previous to signal display on an oscilloscope. Either or both of these changes to the sonar system configuration could produce circumstances under which similar data distributions would appear to be different. Point scatters encountered when plotting target size versus target strength, target strength versus horizontal school area to biomass conversion factor, and target size versus horizontal school area to biomass conversion factor are too wide to detect a relationship between these school parameters.

A distribution of horizontal school area to biomass conversion factors is presented in Figure 6. The distribution is skewed right with an arithmetic mean of 15.16 kg/m^2. While no relationship is as yet demonstrated between individual target strengths and horizontal school area to biomass conversion factors, the data have contributed to a refinement of a general conver-

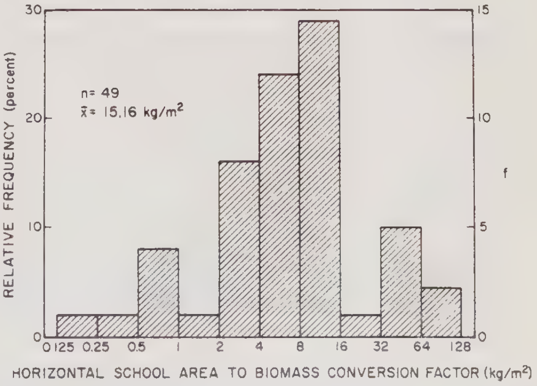

FIGURE 6.—Distribution of horizontal school area to biomass conversion factors obtained from the charter boat experiment.

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[9] Contracts were let for a total of 104 sets assuming 50% success rate for positive sets and a permit was secured from CF&G to land 2,500 tons of anchovy during the experiment. A charter agreement was written establishing criteria for the successful bidders as minimum tonnage bid with the proceeds from any excess tonnage, not to exceed the permit, to be given to the State. In addition, each boat was guaranteed a fixed fee over and above the proceeds from the landed fish.

sion factor based previously on only one data point.

Eight horizontal school area to biomass conversion factors calculated from sets directed by the *Alaska* have a range from 10.14 to 30.22 kg/m^2 with a mean value of 18.42 kg/m^2. The *Alaska* participated in the experiment during the last 2 wk when only large schools were available in shallow water.

AUTOMATED HYDROACOUSTIC DATA ACQUISITION AND PROCESSING SYSTEM

In an effort to reduce observer subjectivity in the collection of large amounts of sonar data necessary for the isolation of sampling errors and biases, a decision was made to develop the capability to automatically count and measure the horizontal dimensions of sonar targets. Peak echo amplitude was also to be measured with the intention of eventually relating it to school compaction and depth.

A digital PDP8/I computer with an additional 16k memory, an analog-to-digital converter and a teletype terminal were acquired on loan from the Naval Undersea Center at San Diego. Using this gear, a project was undertaken which would allow us to do automatically what we were doing manually but with the additional benefits of real-time target strength calculation and rapid raw data processing.

The raw data used for hand target collection is in the form of a paper record containing a field of parallel lines, each line being an incremental distance along the survey track. If the amplitude of the signal is sampled during the recording of one of these lines, at a sample rate of 750 samples/s (velocity of sound/two-way path length), the result is a record of the instantaneous echo amplitude at 1-m increments along a line perpendicular to the survey track.

When several of these lines have been recorded, the result is a data field which is a numerical counterpart of the paper record. Once the word "target" is defined numerically, the number of targets in this field can be counted.

The numerical definitions used for this purpose are:

Threshold (THS) = some signal amplitude greater than the average reverberation or noise level.

Target line = at least five consecutive samples greater than THS, preceded and followed by five samples below THS.

Target block = two target lines which have at least five coincident and consecutive samples greater than THS.

Target = a target block + N additional coincident target lines, bounded by noise (signal less than THS).

The threshold, for the initial program was a predetermined constant. The five sample target line is selected on the assumption that a 5-m target may be the smallest significant unit. The two line target block is selected since random or asynchronous noise greater than THS can cause a target line, but will rarely cause at least five coincident samples on consecutive lines. Three consecutive lines of data are stored in the memory of the PDP8/I computer. As each new line of data is stored it is tested for the presence of target lines. When a target line is found, the amplitude of the samples is compared and the value of the peak amplitude is stored in the first data point location.

The newest data line is then compared with the previous one and any occurrence of a target block is recorded in the block register. The previous data line is compared with the oldest data line and, with the information in the target block register, the following decisions are made:

1. Is the target block the beginning of a new target? If so, assign it a number and record its initial range, final range, and peak amplitude in the temporary target storage register.
2. Is the target block the entire target? If so, store its information in the final target storage field with the current time and the ship's speed.
3. Is the target block part of a previous target? If so, update the temporary storage information.
4. Is the target block the end of a previous target? If so, update the temporary information and store in final storage.

Additional logic decisions are required if two or more previously recorded individual targets later merge to form a single target, or if the inverse should occur.

There are four analog data input lines to the system which are multiplexed and sampled at appropriate times by the analog-to-digital converter. These are:

The start pulse—the trigger pulse for the sonar transmitter.
The sonar signal—the 1,000 cycle band width detected video from the sonar receiver.
The ship's speed—a DC voltage from the ship's log proportional to speed.
The hour mark—a pulse from the ship's precision simplex clock system occurring at the end of each hour.

The start pulse initiates the program, which then counts 200 sample times before recording data. Two hundred fifty samples are then taken between 200 and 450 m, to be operated on by the program as previously described. A running count of the number of start pulses occurring after the beginning of each new hour is kept and used as a time base for all events recorded during that hour. During data reduction, this count is divided into 60 min and used to provide absolute time data.

The ship's speed is recorded with each target, and may be used to calculate the area surveyed. It is used in the data collection program to determine when a hydrographic and/or biological station has been reached and to suspend data recording while on station; start pulses continue to be counted, however, thus the time at the beginning and end of the station is recorded.

In shipboard operation, the system requires no attendance. Prior to leaving the dock, the computer is started, and the hour counter is preset to the current time. The sonar system is then started and may be left in operation 24 h a day or turned off at night. In either case, the data collection program will begin sampling automatically at 0800 each morning and continue until 1600 each afternoon, except while on station. There are six memory storage fields in the PDP8/I of 4,096 words each. One field is used for programming and temporary data storage. The other five fields provide final storage for 3,300 targets, at six data words per target. At the end of the day (1600 h) the data collection program in field zero is replaced by a general computational program used in the PDP8/I called FOCAL. This program change is accomplished automatically from a prerecorded magnetic tape cartridge. With FOCAL programming, the stored target data is now reduced, summarized, and dumped onto peripheral mass storage capable of holding the entire cruise.

When the output is finished, the collection program is reread into field zero, and the computer waits for 0800 h the following morning to again begin data recording.

Field testing of this system was conducted in July 1974, by comparing computer listings of events with the corresponding wet paper records. The system proved to have a greater resolution than was felt necessary and the criteria for a target block changed to two coincident and consecutive samples above threshold. Ten samples below threshold rather than five were judged adequate to terminate a target on any given line. A variable threshold based on an integrated value of volume reverberation is being developed.

The system was field tested under a wide variety of conditions and judged satisfactory for our requirements. Figure 7 describes a cumulative frequency diagram for school count and horizontal school area. A median school size of 30 m agrees with data from previous cruises.

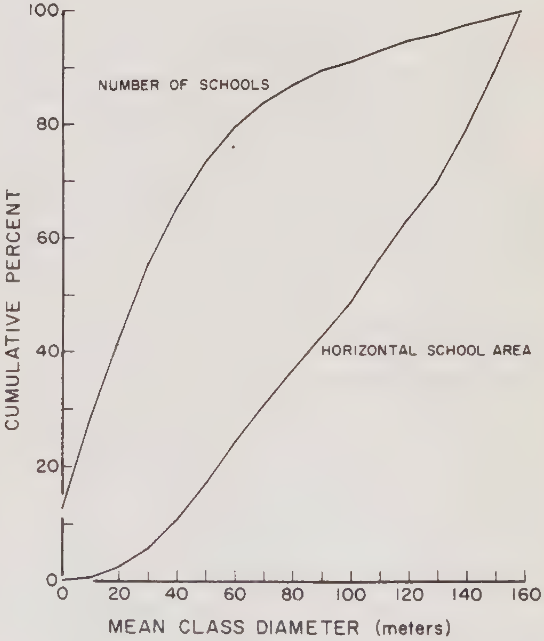

FIGURE 7.—Cumulative frequency diagram of school count and horizontal school area from a sample taken during the field test of an automated sonar system in July 1974.

AUTOMATED SONAR SURVEY

An automated sonar survey of the Los Angeles Bight was accomplished during the last 2 wk of the charter boat cruise. A 721-nautical-mile track (Figure 8) was transected two times providing a 3.4% areal sample of the 11,500-mile^2 Bight. Each track (1.7% sample) was processed as a separate survey.

Appendix Table 3 lists target counts on tracks 1 and 2 by target size and mid-range. Target size refers to the maximum dimension normal to the ship's track and is calculated from the difference between the leading and trailing edges of the echo envelope corrected for the pulse length (15 m at 10 ms pulse length). The first mode, common to both tracks at a target diameter of 30 m, is consistent with earlier data collected by NMFS (approximately 4,500 targets) and CF&G (approximately 23,000 targets). A second mode occurring at a school diameter of 250 m is also common to both tracks. This mode has not been seen before or during any season in any year since sonar activities were initiated off southern California. An explanation for the mode, other than the reflection of an optimum school size, is that it may be a bottom reverberation mode particular to the observation window used on the survey.

Bottom reverberation, as logged by the system, was collected for 2 h over water depths of approximately 100 m during the cruise. Distributions of target size, midrange, and target strength are shown in Appendix Table 4. Notable are two size modes at 50 and 225 m, an optimum midrange of 450 m, and an average target strength of +5 dB.

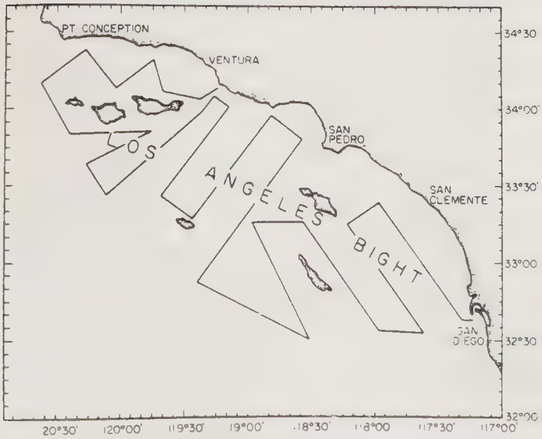

FIGURE 8.—Los Angeles Bight including a 721-mile sonar survey track transected twice, 17-26 September 1974.

Targets contributing to the 250-m size class mode have a midrange mode of approximately 450 m for both tracks 1 and 2. Average target strength was +7 dB for the subsample. This information reinforces the theory that the 250-m size class mode is caused by false targets caused in turn by bottom reverberation. Changes in the sonar system operating parameters (i.e., the enlargement of the observation window and the addition of a time gain circuit) are assumed to be responsible for the variation in system response. These changes were made to facilitate the fish biomass work and will not be in effect during the sonar surveys to be conducted on a series of California Cooperative Oceanic Fisheries Investigations cruises beginning in November 1974. Operating procedures will be the same as used for the initial field of testing of the automated hydroacoustic data acquisition and processing system.

Since those targets which begin or end beyond the observation band are not counted, an edge bias exists which is a function of the target size and the extent of the observation window. Frequencies within target size class intervals were corrected for edge bias by the following formula:

$$N'_d = N_d \frac{500}{500 - d}$$

where N_d = frequency of observation within a given size class
N'_d = frequency corrected for edge bias
d = mean class diameter.

The largest school size corrected for edge bias was 160 m (target size distributions from previous cruises, CF&G and NMFS, indicate that 160 m includes the 99th percentile). Table 4 lists observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes up to a maximum mean class diameter of 160 m.

The total detected school area was 2.6×10^6 m^2 for track 1 and 1.4×10^6 m^2 for track 2. Integrating over the entire survey area by simple proportion, assuming no stratification, and using a conversion factor of 15.16 kg/m^2, biomass estimates of pelagic schooling fish in the Los Angeles Bight were calculated at 2.30×10^6 metric tons and 1.23×10^6 metric tons for tracks 1 and 2, respec-

TABLE 4.—Observed frequencies, edge corrected frequencies, and horizontal school area contributions for size classes (metric tons, mt) up to a maximum of 160 m school diameter.

Class limits (mt)		Mark	*N* (*f*)	*N′*	%Σ*N′*	Cum. %*N′*	*N′A* (mt)^2	%Σ*N′A*	Cum. %*N′A*
Track 1									
−5	5	0	35	35.000	5.171	5.171	0.000	0.000	0.000
5	15	10	74	75.510	11.156	16.327	5,930.557	0.229	0.229
15	25	20	86	89.583	13.236	29.563	28,143.434	1.091	1.321
25	35	30	89	94.680	13.989	43.553	66,925.949	2.594	3.916
35	45	40	68	73.913	10.920	54.473	92,881.869	3.601	7.517
45	55	50	47	52.222	7.715	62.189	102,538.093	3.975	11.493
55	65	60	36	40.909	6.044	68.234	115,667.729	4.484	15.978
65	75	70	30	34.883	5.154	73.388	134,248.290	5.205	21.183
75	85	80	21	25.000	3.693	77.081	125,663.706	4.872	26.056
85	95	90	21	25.609	3.783	80.865	162,922.228	6.317	32.373
95	105	100	18	22.500	3.324	84.190	176,714.586	6.851	39.225
105	115	110	12	15.384	2.273	86.463	146,204.888	5.668	44.894
115	125	120	15	19.736	2.916	89.379	223,218.425	8.655	53.549
125	135	130	13	17.567	2.595	91.975	233,178.346	9.041	62.590
135	145	140	12	16.666	2.462	94.437	256,563.400	9.947	72.538
145	155	150	14	20.000	2.955	97.392	353,429.173	13.703	86.242
155	165	160	12	17.647	2.607	99 999	354,815.170	13.757	99.999
Total			603	676.815			2,579,045.851		
Track 2									
−5	5	0	33	33.000	7.902	7.902	0.000	0.000	0.000
5	15	10	46	46.938	11.240	19.143	3,686.562	0.267	0.267
15	25	20	57	59.375	14.218	33.362	18,653.206	1.353	1.621
25	35	30	50	53.191	12.738	46.100	37,598.848	2.729	4.350
35	45	40	39	42.391	10.151	56.252	53,270.484	3.866	8.217
45	55	50	39	43.333	10.377	66.629	85,084.801	6.175	14.393
55	65	60	24	27.272	6.531	73.160	77,111.819	5.597	19.990
65	75	70	24	27.906	6.683	79.843	107,398.632	7.795	27.786
75	85	80	8	9.523	2.280	82.124	47,871.888	3.474	31.261
85	95	90	8	9.756	2.336	84.461	62,065.610	4.505	35.766
95	105	100	8	10.000	2.394	86.855	78,539.816	5.700	41.467
105	115	110	8	10.256	2.456	89.312	97,469.925	7.074	48.542
115	125	120	6	7.894	1.890	91.202	89,287.370	6.481	55.023
125	135	130	5	6.756	1.618	92.820	89,683.979	6.509	61.533
135	145	140	9	12.500	2.993	95.814	192,422.550	13.967	75.500
145	155	150	4	5.714	1.368	97.182	100,979.763	7.329	82.830
155	165	160	8	11.764	2.817	99.999	236,543.446	17.169	99.999
Total			376	417.576			1,377,668.706		

tively. Identification of the fish is not yet possible on a routine basis. However, it is assumed that the majority of schooling fish in the Los Angeles Bight are northern anchovy (Smith 1972; Squire 1972; Mais 1974).

DISCUSSION

It is our impression that the ultimate value of sonar mapping is its potential to reconstruct geographic patterns of school distributions at a moderate cost of time both in data collection and data reduction. However, before this potential can be fully realized, several problems must be recognized, investigated, and placed in proper perspective.

With regard to counting and sizing targets:

1. An edge bias has been described which will be present with any sonar system designed to count and size schools. The determination of effective detection ranges establishes a finite observation band. Larger schools tend to be undersampled relative to smaller schools; in terms of school area the bias may be significant.
2. Increasing the observation band would tend to reduce the effect of edge bias. However, the effects of target size and target strength on maximum ranges of detection should be investigated before defining the observation band. Undersampling small schools may be acceptable when considering their area contribution.
3. Effective detection ranges may also be limited by inhomogeneities in the medium caused by short-period internal waves. Smith (see footnote 3) investigated this phenomenon and suggested the only practical solution is a statistical approach

whereby the number of sound velocity profiles taken in an area-time stratum would be limited to the number of samples necessary to reduce the standard error to a uniform value for all strata. A probability of detection diagram could then be constructed from the ray trace analyses and target counts corrected by range. We have not so far considered these effects in our area of operation, however, the implication of undersampling should be investigated when designing a serious stock assessment survey using sonar.

4. Diurnal and seasonal variations in school sizes can be expected. In order to properly evaluate their affect on a stock assessment scheme the period and amplitude of these variations must be measured. The collection of a data base sufficient in size to detail these changes, as well as geographic distribution patterns by season, was the primary motivation in designing an automated data collection system.
5. While it appears that influences of bottom topography on school distribution may be neglected, there is no reason to expect areal distributions to be uniform. In fact, there is evidence from aerial reconnaissance, sonar transects obtained at long ranges (2,500 m), and fishermen that fish schools may be distributed in a highly contagious fashion similar to the distributions of fish eggs and larvae. In our opinion, this is a most important consideration in arriving at an optimum survey design. Smith[10] and MacCall[11] have approached the problem by direct measurement and simulation modeling and suggest a transect spacing of 15 miles as adequate to reconstruct groups of anchovy schools off southern California.
6. Holliday (1972, 1974) demonstrated the feasibility of sizing individual fish within schools and provided information which would aid in species identification. A development of these techniques as practical additions to a sonar survey system would reduce a presently loosely quantified factor, i.e., the percent of detected schools which can be expected to be the target species of a survey.

With regard to school target strength:

1. The target strength of an individual fish is an essential element in interpreting the measured target strength of a school. At the frequencies commonly used for sonar mapping we can expect interference of energy reflected from the various scattering parts of a fish. This makes the target strength of a fish strongly aspect dependent. Unfortunately there is presently no method of acoustically determining the aspect of individuals in a school and hence their effective target strength. As such, the maximum dorsal or side aspect target strength is generally an overestimate and the use of these values in interpreting school target strengths results in an underestimate of the number of individual scatterers.
2. We may also expect multiple scattering, shadowing, and attenuation within a school. These effects may tend to reduce or enhance the target strength of a school and cannot be evaluated until we know the effective contribution of the fish taken as individual scatterers. Love (1971) stated that the quantification of a fish school using its target strength is possible because the target strength of a school depends on the average size, number, distribution, and aspect of the individuals in the school. If the effects of the distribution of fish in space and their aspect can be removed, we may assume an average size and estimate their numbers.
3. We have assumed spherical spreading losses which may only be expected in a three-dimensional homogeneous fluid. In fact, the upper mixed layer, in which we operate our sonar, is characteristically bounded by density discontinuities which reflect and refract sound waves. The actual path of transmitted and target-reflected sound waves may not be direct as implied in the use of spherical transmission losses.

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[10] Smith, P. E. 1975. Precision of sonar mapping for pelagic fish assessment in the California Current area. SWFC Administrative Report No. LJ-75-60. Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

[11] MacCall, A. 1975. Anchovy population survey simulation. Contribution No. 4, CalCOFI Anchovy Workshop, July 1975. Document on hand at the Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

Continuing development of acoustic stock assessment techniques rests on the comparison of measurements and the best available theoretical models for target strength and fish school biomass. Improved instrumentation, particularly data logging and processing equipment will make the comparison more timely and useful. The existing system will be used seasonally over the entire California Current survey area (about 200,000 nautical miles^2) in 1975. It is intended that the data base thus furnished will allow a balanced approach to such biological problems as migration and patchiness of fish schools in the context of better theory and instrumentation.

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APPENDIX TABLE 1.—Topographic breakdown of Los Angeles Bight by four classes of bottom configuration (zone) and distribution of design and actual sampling effort.

Zone and name	Area (nautical mile^2)	Total area (%)	Sampling effort Design (%)	Sampling effort Actual (%)
Banks:				
Thirtymile Bank	44.8			
Fortymile Bank	39.6			
Tanner Bank	50.2			
Osborn Bank	13.4			
San Clemente Bank	37.3			
San Nicolas Bank	125.4			
Santa Rosa N. Bank	17.7			
Santa Rosa S. Bank	34.0			
Coronado Bank	19.1			
Santa Barbara Bank	72.7			
Santa Cruz Bank	79.3			
Lasuen Seamount	13.2			
Total	546.7	4.8	14.4	9.4
Basins:				
San Clemente Basin	91.7			
Catalina Basin	540.8			
San Nicolas Basin	497.3			
San Diego Trough	264.2			
San Pedro Basin	145.6			
Santa Monica Basin	490.3			
Santa Cruz Basin	213.2			
Santa Barbara Basin	733.2			
Total	2,976.3	25.9	27.4	34.4
Escarpments and canyons:				
Coronado Escarpment and Canyon	37.3			
Catalina Escarpment	99.5			
San Clemente Escarpment	97.4			
San Diego Escarpment	38.9			
San Pedro Escarpment and Redondo Canyon	33.4			
San Nicolas Escarpment	34.2			
Santa Cruz Escarpment and Canyon	75.4			
Santa Monica Escarpment	15.5			
Santa Barbara Escarpment	23.3			
Cortez Escarpment	12.4			
Total	467.3	4.1	24.1	23.7
Slopes		65.2	34.1	32.5

APPENDIX TABLE 2.—Detected targets and target densities for four classes of bottom topography (zone) in the Los Angeles Bight.

Zone and name	No. targets obs.	Linear nautical miles surveyed	Target density (targets/nmi^2)
Banks and seamounts:			
Thirtymile Bank	3	12.40	1.79
Fortymile Bank	18	16.99	7.85
Tanner Bank			
Osborn Bank	1	6.19	1.20
San Clemente Bank			
San Nicolas Bank			
Santa Rosa Bank			
Santa Rosa S. Bank			0
Coronado Bank	0	8.0	0.75
Santa Barbara Bank	2	19.8	0
Santa Cruz Bank	0	21.59	0
Lasuen Seamount	14	9.59	10.81
$\overline{\ln x}$ excluding zero values			0.9835
$S_{\ln x}$			1.1758
Basins and troughs:			
San Clemente Basin	43	22.60	14.09
Catalina Basin	84	83.99	7.41
San Nicolas Basin	135	44.19	22.63
San Diego Trough	94	58.19	11.84
San Pedro Basin	4	21.40	1.38
Santa Monica Basin	1	31.59	0.14
Santa Cruz Basin	0	23.4	0
Santa Barbara Basin	0	37.4	0
$\overline{\ln x}$ excluding zero values			1.4325
$S_{\ln x}$			1.9237
Escarpments and canyons:			
Coronado Escarpment and Canyon	1	19.40	0.38
Catalina Escarpment	15	28.19	3.94
San Clemente Escarpment	3	40.39	0.55
San Diego Escarpment	172	51.53	24.73
San Pedro Escarpment and Redondo Canyon	25	19.80	9.35
San Nicolas Escarpment	38	14.99	18.78
Santa Cruz Escarpment and Canyon	4	33.18	0.89
Santa Monica Escarpment	0	11.00	0
Santa Barbara Escarpment	0	12.4	0
Cortez Escarpment	6	6.79	6.55
$\overline{\ln x}$ excluding zero values			1.2431
$S_{\ln x}$			1.6145
Slopes	0	9.40	0
	21	20.19	7.71
	0	6.00	0
	0	6.80	0
	0	5.00	0
	0	7.99	0
	5	22.80	1.62
	0	7.80	0
	4	7.20	4.16
	9	12.39	5.38
	65	30.69	15.69
	46	16.59	20.54
	23	9.00	18.93
	21	6.20	25.09
	7	15.20	3.41
	20	4.00	37.04
	0	3.60	0
	0	3.20	0
	1	55.00	0.13
	0	5.40	0
	22	11.20	14.55
	0	27.20	0
	2	17.20	0.86
	17	15.51	8.12
$\overline{\ln x}$ excluding zero values			1.7850
$S_{\ln x}$			1.5365

APPENDIX TABLE 3.—Target counts by size and midrange detected on an automated survey of the Los Angeles Bight (tracks 1 and 2) during September 1974.

Size (m)	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500	500-550	550-600	Total
<5	3	3	6	11	17	6	3	5	7	6	67
6- 15	4	5	7	16	26	18	7	13	14	10	120
16- 25	1	8	11	23	24	16	15	11	17	17	143
26- 35	4	3	4	15	29	21	15	11	22	15	139
36- 45		2	4	9	24	14	11	13	19	11	107
46- 55		1	3	7	8	10	10	10	21	16	86
56- 65		3	2	4	11	2	9	6	16	7	60
66- 75			1	2	7	2	7	8	27		54
76- 85		1		1	1	4	6	5	11		29
86- 95			1	3	3	2	3	2	15		29
96-105					2	2	3	4	15		26
106-115				1	1	3	3	4	8		20
116-125				3	1	2	4	4	7		21
126-135						4	1	5	8		18
136-145				1	2	3		8	7		21
146-155				1		5	5	3	4		18
156-165			1		4	3	2	5	5		20
177-175			1		1		3	6			11
176-185						2	9	11			22
186-195					1	1	11	7			20
196-205				4	1	3	12	8			28
206-215					2	2	11	10			25
216-225					1	5	14	23			43
226-235					2	3	27	25			57
236-245						3	26	22			51
246-255					1	3	31	27			62
256-265						3	34	14			51
266-275						1	21				22
276-285						2	24				26
286-295						1	23				24
296-305				1	1	2	22				26
306-315						3	16				19
316-325				1	1	1	8				11
326-335						3	4				7
336-345						1	1				2
346-355						3					3
356-365						2	1				3
366-375						3					3
376-385						4					4
386-395						1					1
Total	12	26	41	103	171	169	402	270	223	82	1,499

APPENDIX TABLE 4.—Bottom reverberation by detected size, midrange, and target strength from data collected during 2 h in 100 fathoms on 7 September 1974.

Item	Mark	f	Relative %	Item	Mark	f	Relative %
Size	25 m	9	5.4	Midrange	480	15	8.9
	50	24	14.3		500	7	4.1
	75	11	6.5		520	7	4.1
	100	9	5.4		540	1	0.6
	125	8	4.8		560	1	0.6
	150	10	6.0	Target strength	−2dB	1	0.6
	175	18	10.7		−1	1	0.6
	200	26	15.5		0	4	2.4
	225	24	14.3		1	11	6.5
	250	23	13.7		2	18	10.7
	275	6	3.6		3	21	12.4
	300	0	0		4	25	14.8
Midrange	340 m	5	3.0		5	28	16.6
	360	7	4.1		6	25	14.8
	380	6	3.6		7	6	3.6
	400	9	5.3		8	9	5.3
	420	25	14.8		9	7	4.1
	440	44	26.0		10	8	4.7
	460	42	24.9		11	5	3.0

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THE ROCK WRASSE, *HALICHOERES SEMICINCTUS*, AS A CLEANER FISH[1]

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What may have been one individual rock wrasse, *Halichoeres semicinctus*, was observed over 10 months cleaning other fishes at Santa Catalina Island. Cleaning is an insignificant activity for rock wrasse in general, but was a major activity of the individual involved in each of these observations. Cleaning activity of the rock wrasse is similar in most respects to that of its relative, the señorita, *Oxyjulis californica*.

INTRODUCTION

The rock wrasse, *Halichoeres semicinctus*, which is numerous over algal-covered substrata in shallow near-shore waters off southern California, looks much like another wrasse, the señorita, *Oxyjulis californica*, which is even more numerous in the same area. Although the señorita is the predominant cleaner fish in California (Limbaugh 1961; Hobson 1971), the rock wrasse has not been known to clean.

Cleaning, or removing by mouth, ectoparasites and other deleterious materials from the bodies of other animals (Feder 1966), cannot be a major activity of the rock wrasse. During an 18-month field study of cleaning symbiosis at La Jolla, California (Hobson 1971), I failed to see this species clean. Nor did I see it clean during extensive incidental observations over 12 years (1961 to 1973) in areas frequented by this fish. Occasionally I saw other fishes respond to an approaching rock wrasse by hovering motionless in the manner of fishes that solicit cleaning (Feder 1966), but always they were unsuccessful in eliciting service. Furthermore, in other accounts of cleaning symbiosis in California (e.g. Limbaugh 1955; Gotshall 1967) the rock wrasse has remained unimplicated in cleaning symbiosis, either as cleaner or as a client.

Recently, however, I observed the rock wrasse cleaning other fishes, including members of its own species, near Isthmus Cove, Santa Catalina Island. The activity was witnessed on four occasions over 10 months at a single location in 5 m (17 ft) of water along the inner margin of a kelp, *Macrocystis*, forest.

My feeling is that all these observations involved the same individual cleaner. I cannot be positive of this, but two facts lead to this impression. First, the cleaner each time was an adult male, about 150 mm (6 inches) long, and, although the species was numerous throughout the area, males differ markedly in coloration with size, and only a relatively few resembled the cleaner. Second, despite being widespread and frequently observed, this species has only been seen cleaning at this one spot, a circumstance that seems best explained by the one-individual hypothesis.

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OBSERVATIONS

June 1973

I first observed the rock wrasse cleaning during midafternoon in June 1973. After recognizing that this individual was a cleaner, I followed it for 30 min as it circled slowly back and forth within an area about 10 x 40 m (33 x 132 ft), 1 to 2 m (3 to 7 ft) above the sea floor, and then finally lost contact with it amid the kelp. During the observations, it approached, inspected, and then frequently cleaned, the external body surfaces of a succession of fishes of several species (recounted below). Between cleaning bouts, the cleaner swam slowly from one part of its operating range to another, and during these times picked at drifting debris four times and once inspected an algal-covered rock. Mostly, however, it appeared alert for cleaning opportunities.

Repeatedly during its leisurely meandering, the cleaner abruptly changed course and swam with accelerated movements directly toward a fish that was as much as 5 m (17 ft) away. Individuals of several species were thus approached, all of them at the time active in ways characteristic of their kind. Every time the cleaner neared they abruptly assumed the hovering attitude of fishes that solicit cleaning. The cleaner then swam to each one, made a close visual inspection, and then frequently plucked one or more times at their body surfaces.

During this period, when cleaning was clearly its major activity, the rock wrasse serviced individuals of three species: opaleye, *Girella nigricans;* halfmoon, *Medialuna californiensis;* and black perch, *Embiotoca jacksoni.* Of eight opaleyes approached and inspected, it cleaned four, plucking at their bodies one to three times. It cleaned both halfmoons that it approached and inspected, plucking at each more than 10 times. Of two black perch approached and inspected, it cleaned one, plucking at its body twice.

Several other incidents during the observation period are noteworthy. Once the cleaner swam close to another rock wrasse, which paused and erected its dorsal fin as if to solicit cleaning, but the cleaner then passed by without apparent interest. Another time a garibaldi, *Hypsypops rubicundus*, swam up alongside the cleaner as it attended a halfmoon, and, although the garibaldi hovered head down in soliciting fashion just a few cm away, the cleaner gave no overt response.

August 1973

During my next visit to the same location, 1 month later, I again saw a rock wrasse cleaning. This time the cleaner was attending another member of its own species that hovered in a regular horizontal attitude, except that its dorsal fin was erected. The cleaner plucked at the base of this fin once, then swam off. Immediately it moved to another rock wrasse nearby, but, though this one stopped swimming and erected its dorsal fin, the cleaner passed by after only a brief inspection. Two more essentially identical encounters followed in succession, seconds apart, each with a different rock wrasse. Then the cleaner approached a garibaldi, which failed to respond, and then a kelp bass, *Paralabrax clathratus*, which also failed to respond. At this point, only 4 min after the observations had begun, I lost track of the cleaner amid a stand of kelp. Although I searched the area for an additional 25 min, I saw no further cleaning.

February to March 1974

Six months later, on February 14, 1974, James R. Chess (Tiburon Laboratory, National Marine Fisheries Service) was diving in the same location and saw a male rock wrasse about 150 mm (6 inches) long cleaning a garibaldi (pers. commun.). This prompted me to follow up the observations I had made during the previous summer. The earlier observations had been incidental to other work, but now I visited the same area once during each of the following 5 weeks specifically to look for cleaning by the rock wrasse. On the first visit (1200 hr, February 26), underwater visibility was so reduced by suspended material that the effort was abandoned after 10 min of fruitless search.

On the next visit (1300 hr, March 4), conditions were better and after only 5 min in the water I spotted a rock wrasse cleaning a garibaldi. During the next 17 min, I followed the cleaner as it meandered over a relatively large area, about 20 x 75 m (72 x 248 ft) swimming about 1 m (3 ft) above the sea floor. Its course brought it within about 5 m (17 ft) to 16 garibaldis, and every time but once the cleaner swam to the garibaldi, which then invariably assumed the attitude of a fish soliciting cleaning. After a brief visual inspection, the cleaner plucked at the body of each garibaldi 1 to 3 times, then continued on its way. During this time, the cleaner passed close to many other fishes (including individuals of all species previously noted being cleaned by the rock wrasse), but failed to show interest in any of them. Three times it plucked at drifting debris, and once it inspected, but did not pluck at the benthos; otherwise, it seemed interested only in cleaning garibaldis. Finally, I lost contact with the cleaner amid benthic vegetation.

The remaining visits were less fruitful. I looked unsuccessfully for the cleaner on the third and fifth visits (1430 to 1500 hr on March 11, and 1215 to 1245 hr on March 20), even though visibility underwater exceeded 15 m (50 ft). However, after 15 min in the water on the fourth visit (1300 to 1345 hr on March 14), I spotted a rock wrasse inspecting a garibaldi. This time I carried a camera, intending to photograph the activity. As I approached to within close range, however, the rock wrasse, still inspecting the garibaldi, abruptly withdrew without cleaning. I kept the rock wrasse in view for 6 min before losing contact, and during this time it approached and inspected 5 garibaldis. As it closed in on each of these fish, I approached closely for the photo, and each time the rock wrasse broke away without cleaning, probably in alarm at my close approach. Although it did not actually clean, it approached only garibaldis, showing no overt interest in the many other species present.

REMARKS

Cleaning as a Characteristic of Only Certain Individuals

Whether or not one shares my feeling that just one individual cleaner performed during these events, the observations complement, and to an extent suggest modifying, some of my previous thoughts on cleaning symbiosis in California.

My earlier report on California cleaners (Hobson 1971) distinguished between habitual and incidental cleaners. Cleaning is a widely acknowledged major activity of all those species considered to be habitual cleaners. In citing the señorita as an example, I pointed out that while most señoritas apparently do not clean, at least not at any given time, those that do are nevertheless relatively numerous and widespread. On the other hand, the species considered to be incidental cleaners have only rarely been seen cleaning, even though they are well-equipped to pluck tiny organisms from a substrate, and include some of the most frequently observed fishes in southern California. Among species considered incidental cleaners were pile perch, *Damalichthys vacca,* rainbow perch, *Hypsurus caryi,* and white perch, *Phanerodon furcatus.* These species had been identified as cleaners by Limbaugh (1955, 1961), Gotshall (1967), and Hobson (1971). Sightings of cleaning by these species have been rare, it was reasoned, because to them cleaning is just an infrequent incidental adjunct to their regular foraging. Based on the cleaning activity of the rock wrasse, however, the infrequency of these observations may relate, at least in some instances, to there being relatively few cleaning individuals among these species, rather than to the species members in general cleaning infrequently. Far from being an occasional, incidental event, cleaning may at times be the major activity of these particular individuals, as important to them as to any of those others earlier distinguished as habitual cleaners.

One wonders how many frequently practiced activities of individuals are in fact uncharacteristic of other members of their species. The cleaning rock wrasse was noticed apart from other rock wrasse only because cleaning is so obvious. It seems probable that every individual exhibits certain behaviors, perhaps more subtle than cleaning, that set it apart from others of its kind, a fact that deserves more attention.

Some Comparisons With The Señorita

Cleaning interactions involving señoritas and rock wrasse generally are initiated by the cleaners. We might wonder why fishes that receive this cleaning fail to seek out the cleaners, just as many fishes seek out cleaners on tropical reefs (Feder 1966). Obviously señoritas and rock wrasse are welcomed as cleaners, judging from the way fishes that receive them promptly hover motionless with fins erected. It is unlikely these fishes would assume such vulnerable attitudes unless they benefited from the cleaner's actions. Why then do fishes cleaned by señoritas and rock wrasse always wait for the cleaners to identify themselves by making the first move? The explanation offered for situations involving the señorita (Hobson 1971) would seem even more applicable to the rock wrasse. That is, fishes probably are unable to distinguish cleaning rock wrasse from among the many more non-cleaning rock wrasse around them. The tropical fishes that routinely initiate encounters with cleaners generally approach highly specialized forms like the Hawaiian cleaner wrasse *Labroides phthirophagus* (Losey 1971). Generally, these cleaners center their activity around well-defined stations, so that fishes know precisely where to go for service; furthermore, because most individuals of the cleaning species are themselves cleaners, even random attempts to solicit service from individuals in the population at large would have a reasonably good chance for success. This would be untrue of random attempts to solicit cleaning from either the rock wrasse or señorita.

Cleaning señoritas tend to clean members of just one species during a given period of activity (Hobson 1971). In attempting to explain this situation, I pointed out that because the señorita generally initiates its cleaning encounters it can select its clients. Each potential client-species differs in appearance and behavior, so that each presents a distinctive target to the approaching cleaner. Although these differences often seem subtle, they probably influence the cleaner's choice of clients.

Applying the same reasoning to the cleaning rock wrasse, it is not surprising that during February and March the rock wrasse approached and cleaned only the bright-orange garibaldi, a fish readily distinguished from all others in its habitat. During the previous June, however, the rock wrasse had cleaned several species in succession: opaleye, halfmoon and black perch. These three species are similar, all being deep-bodied, dark-hued fish that often swim close above the sea floor, and so they may be a measure of the extent the cleaner generalizes when selecting clients. Perhaps significantly, the garibaldi that solicited cleaning at this time was ignored. During the August observations, the rock wrasse showed interest in a more diverse assortment of fishes, although only other members of its own species responded to this interest. The significance of this apparent inconsistency is difficult to assess, however, because the session was so brief (4 min).

Although observations made since my 1971 report continue to support the contention that cleaning señoritas tend to clean members of just one species during an undetermined period of time, I have seen a few señoritas clean several dissimilar species in succession. Apparently, the extent to which señoritas generalize in selecting clients, like the incidence of cleaning, varies between individuals.

If, in fact, one individual rock wrasse performed all the cleaning described in the present report, then the observations indicate that, although its concept of a cleaning target remained unchanged over at least 1 month (February 14 to March 14), there had been a change between the previous June and August, and another between August and February.

In the guts of señoritas, ectoparasites that presumably had been taken by cleaning frequently occur in blocks sharply delimited from foods obviously unrelated to cleaning (Hobson 1971). I consider this evidence that these individuals had cleaned intensively for a while, abruptly shifted to other modes of feeding, and then later returned to cleaning. It remains unknown whether or not the cleaning rock wrasse similarly alternates between protracted bouts of cleaning and non-cleaning modes of feeding.

ACKNOWLEDGEMENTS

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TROPHIC INTERACTIONS AMONG FISHES AND ZOOPLANKTERS NEAR SHORE AT SANTA CATALINA ISLAND, CALIFORNIA[1]

Edmund S. Hobson and James R. Chess[2]

ABSTRACT

Predation pressures from fishes have influenced major evolutionary trends among shallow-water zooplankters, as concluded from study at Santa Catalina Island, Calif. The predominant zooplanktivorous fishes near shore are actinopterygians, an evolutionary line that has centered around generalized visually feeding, large-mouthed predators. Historically, zooplankters threatened by these fishes have faced selective pressures favoring reduced size, transparency, and/or nocturnal planktonic habits. At present, most zooplankters in the nearshore water column by day are very small (<2 mm, approximately); included are cladocerans, copepods, and various larval forms. Their small size precludes capture by most large-mouthed fishes, thus providing protection in daylight, when the visual sense of generalized predatory fishes is most effective. Larger zooplankters in the water column by day, for example chaetognaths, tend to be transparent. The advantage of transparency to organisms threatened by visually feeding predators is obvious, and is only briefly mentioned here. Zooplankters having sizes (most >2 mm) and other features making them vulnerable to large-mouthed fishes tend to enter the water column only at night, when darkness offers some security from visually feeding predators. Included are polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, tanaids, isopods, and carideans.

Because successful defensive features of prey create pressures that modify the offensive features of predators, the tendencies toward reduced size and nocturnal habits among zooplankters have generated appropriate adaptations among planktivorous fishes. Fishes that prey as adults on zooplankters during the day (e.g., blacksmith, *Chromis punctipinnis*) have specialized features, including a small highly modified mouth, that permit even relatively large individuals to take the tiny organisms which constitute the daytime zooplankton. Some other fishes are diurnal planktivores only as small juveniles and assume different feeding habits as they grow larger (e.g., kelp perch, *Brachyistius frenatus*; señorita, *Oxyjulis californica*; smaller juvenile olive rockfish, *Sebastes serranoides*). Fishes that prey on zooplankters at night (e.g., larger juvenile olive rockfish; kelp rockfish, *Sebastes atrovirens*; queenfish, *Seriphus politus*; walleye surfperch, *Hyperprosopon argenteum*; and salema, *Xenistius californiensis*) take the larger organisms that join the zooplankton after dark. In their feeding morphologies and body form, these large-mouthed fishes have diverged less than their diurnal counterparts from the generalized predators that give rise to them all. They have, however, acquired specialized features, including large eyes, suited to detect and capture prey in the dark.

Interactions among predators and their prey are best recognized by viewing assemblages of animals that occur together in nature. Furthermore, many trophic interactions become apparent only upon considering the changes that occur from day to night, and from one season to another. These convictions shaped studies of feeding relations among tropical reef fishes undertaken between 1962 and 1970 (Hobson 1965, 1968, 1972, 1974), and similarly influenced work done in warm temperate waters from 1972 to 1975. This more recent work centered on the inshore habitats at Santa Catalina Island, Calif. (lat. 33°28′N, long. 118°29′W), where most of the attention was directed at fishes that forage on the benthos (Hobson and Chess in prep.). The present report, however, deals with that segment of the work involving certain fishes and trophically related zooplankters that interact in the water column near shore.

Only a few studies have considered feeding habits in natural assemblages of marine fishes. Limbaugh (1955) and Quast (1968) made the major contributions in southern California, but these important studies represent only a beginning.

The present study goes beyond earlier investigations by considering the organisms taken by the fishes as prey against a broader consideration of the array of similar forms present that would seem to have been equally accessible. The selection of specific prey, however, is only partially developed in discussing these data. Selectivity will

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be treated in depth later (Hobson and Chess in prep.), when these data can be reconsidered along with the data on organisms simultaneously accessible on the sea floor and other substrata, as well as in the water column above habitats different from those described here.

TERMINOLOGY

In this report, the term zooplankton encompasses all the varied small organisms we collected with a plankton net during day and night, and (most important to this study) which proved to include the major foods of a well-defined assemblage of fishes. All the organisms that we consider within this definition belong to groups included in most general accounts of the zooplankton (e.g., Newell and Newell 1963; Wickstead 1965).

Nevertheless, some planktologists would exclude from zooplankton forms like large caridean shrimps that irregularly enter the water column at night. But among crustaceans such distinctions fail to establish where, along the continua of size, mobility, and time spent in the water column, forms like large carideans are apart from those minute calanoid copepods that are zooplankters by any definition. A number of terms defining certain ecological categories among zooplankton have been proposed (e.g., holoplankton, meroplankton, tychoplankton, etc.), but while such terms are useful in certain contexts, we have seen none that define categories meaningful to the concepts developed in this paper (see Discussion).

STUDY AREA

The study area is 25 to 75 m off the western shore of Big Fisherman's Cove (Figure 1). Most of the area is open water about 5 to 15 m deep over a sandy sea floor largely overgrown by the brown alga *Dictyopteris zonariodes* (most of which is anchored to tubes of the polychaete *Chaetopterus variopedatus* (Figure 2)). From the seaward edge of the study area, the bottom falls sharply to the greater depths (more than 30 m) that lie at the center of the cove. Shoreward, and at the mouth of the cove, lies a forest of giant kelp, *Macrocystis pyrifera*. This large brown alga grows to the water's surface from a rocky bottom that slopes up to the shoreline from depths of about 8 m (Figure 3). Water temperatures during the study ranged from lows around 12°C in spring, to highs around 20°C in late summer.

FISHES STUDIED

The fishes studied are those that, during either day or night, swim in the water column and feed principally on zooplankters. They are:

- Family Scorpaenidae: scorpionfishes
  - Olive rockfish, *Sebastes serranoides* (Eigenmann and Eigenmann)
  - Kelp rockfish, *S. atrovirens* (Jordan and Gilbert)
- Family Pomadasyidae: grunts
  - Salema, *Xenistius californiensis* (Steindachner)
- Family Sciaenidae: drums
  - Queenfish, *Seriphus politus* Ayres
- Family Embiotocidae: surfperches
  - Walleye surfperch, *Hyperprosopon argenteum* Gibbons
  - Kelp perch, *Brachyistius frenatus* Gill

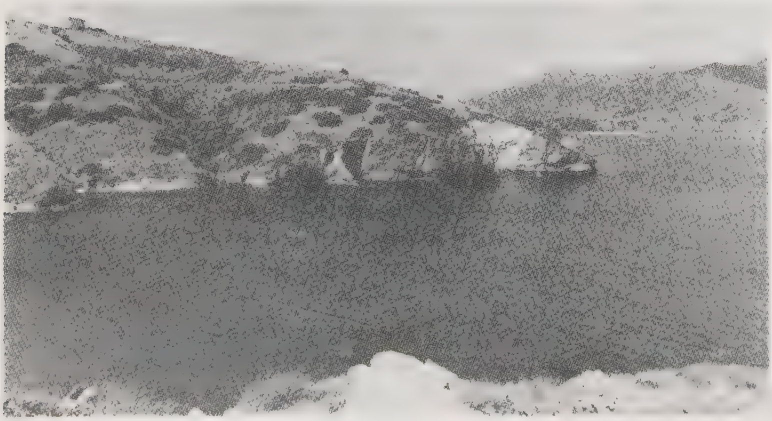

FIGURE 1.–Big Fisherman's Cove, Santa Catalina Island. The study site lies near the opposite shore, between the buoy and the headland.

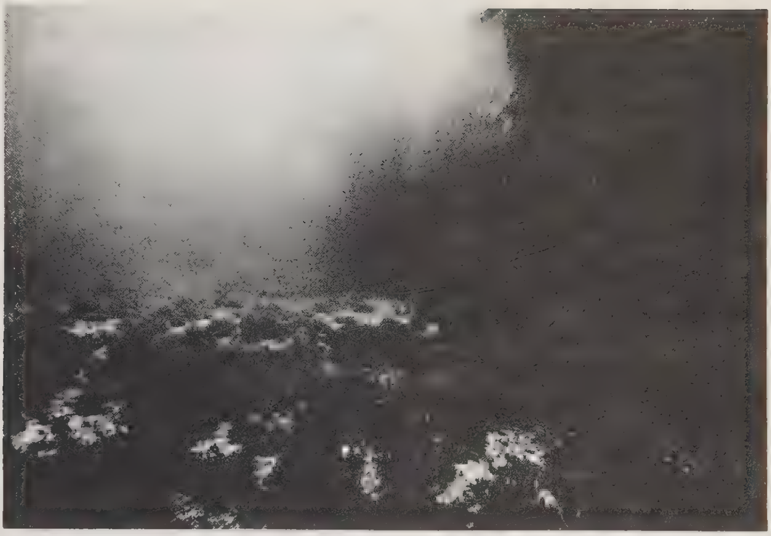

FIGURE 2.–The *Dictyopteris* field, bordered by the *Macrocystis* forest.

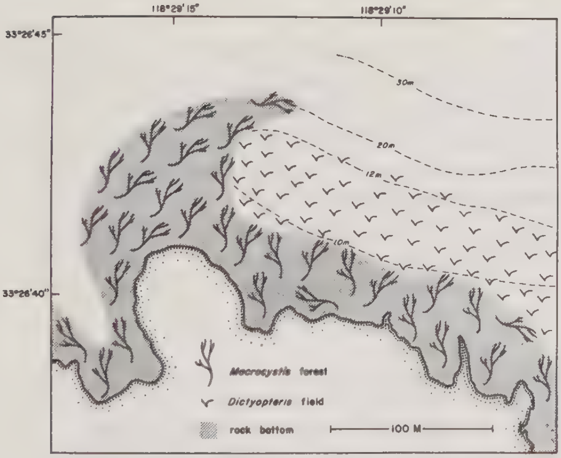

FIGURE 3.–The study area at Santa Catalina Island.

Family Labridae: wrasses
  Señorita, *Oxyjulius californica* Günther)
Family Pomacentridae: damselfishes
  Blacksmith, *Chromis punctipinnis* (Cooper)

Only two other species in the study area have similar zooplanktivorous habits: the topsmelt, *Antherinops affinis* (Ayres), and the shiner perch, *Cymatogaster aggregata* Gibbons. These two, however, are more characteristic of other habitats, where the species composition of available prey is different. Although for this reason they will be described in separate reports later, their activities are entirely consistent with what is reported and discussed below.

METHODS

Direct Observations

We used scuba and snorkeling (167 h underwater) to observe activity of the fishes and trophically related organisms during all periods of day and night. Except when collecting specimens, we tried to avoid influencing the organisms or their environment.

Collecting Zooplankters

During the same period that we collected fishes for the food-habit study, organisms in the water column that might be their prey were sampled with a 1-m plankton net (0.333-mm mesh) that we pushed through the water for 5-min periods (Figure 4). In this way, a series of paired collections sampled the waters above the *Dictyopteris* field during September 1973, February 1974, and May 1974. Of each pair, the first sampled the water column midway between the water's surface and the sea floor (in 10 to 15 m of water); and the second, which followed immediately, sampled the base of the water column to within about 10 cm above the bottom. During each sampling month, we made a set of eight collections–four at full moon, and four at new moon. Each set included a pair at night (between 2 and 4 h after last evening light), and a pair the following day (between 1200 and 1400 h). In addition, we made one set of collections in the kelp forest bordering the study

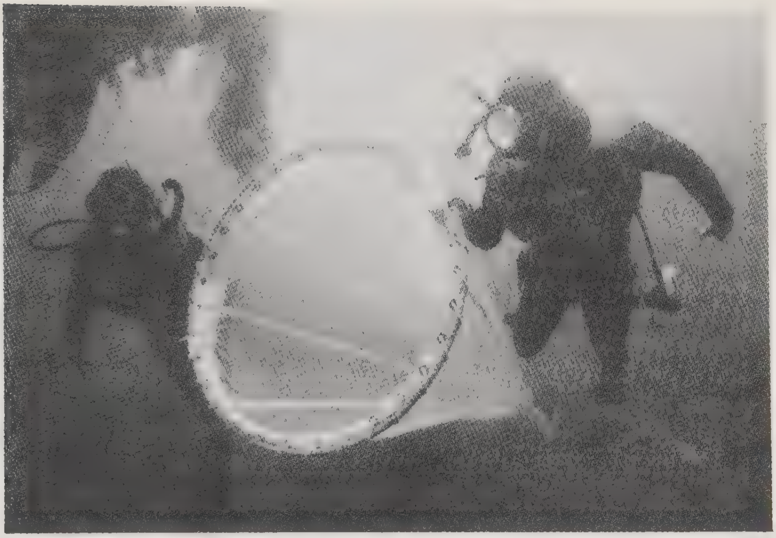

FIGURE 4.–Collecting plankton at middepths.

area: a pair at night, under a full moon (when there was enough light to maneuver among the kelp columns), and a pair the following midday.

Because diving lights probably influence organisms in the water column, we turned them off when collecting with the plankton net at night. At these times the moon provided ample light to navigate when it was present, but on dark nights we depended on the luminous dials of our compasses and depth gauges.

Collecting Fishes

To determine the food habits of the fishes, we speared 521 specimens of the eight species and then examined their gut contents. All specimens were taken in the study area between September 1973 and May 1974–the same period over which we sampled the zooplankton. Most of these specimens were collected either at night, within the 2 h before sunrise, or during the afternoon–times that best show differential day or night feeding. All measurements of fish size noted in this report are of standard length.

Sample Analysis

Zooplankton Samples

Generally the samples were analyzed within 2 wk after collection. Sample volumes, which ranged from 0.2 to 36.0 ml ($\bar{x} = 8.3$), were determined after they had settled for 5 min in a graduated cylinder. The entire sample was analyzed when its volume was less than 5 ml. When the sample was larger, 5-ml aliquots were analyzed, and numbers for the entire sample then extrapolated. Whenever less than the entire sample was analyzed, the balance was searched for forms missing from the aliquot; when found–always in small numbers–these were counted and added to the list.

Fish Gut-Content Samples

The digestive tract of each fish specimen was removed immediately after collection, and preserved in a 10% Formalin[3] solution. For analysis, the contents were examined under a binocular dissecting microscope, and, when necessary, a binocular compound microscope. A note was made of the position in the digestive tract of the various items. A list was then composed of the items in the gut, with the species identified when feasible. The following data were then noted for the items in each listed category: 1) their number; 2) their size range; 3) the extent they had been digested (subjectively assessed on a scale of five, from fresh to well-digested); and 4) an estimate of their representation in the gut as percent by volume of the contents.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Volumes of Zooplankters, Day and Night

Our collections with the plankton net were too few, and spaced over too much time, to attach much significance to the differences in volume between various samples. Nevertheless, certain characteristics probably are meaningful.

The volumes of samples taken day and night at full moon compared with day and night at new moon are as follows: FULL MOON–daytime, middepths ($n = 3$): 1 to 18 ml, $\bar{x} = 8.3$; daytime, near bottom ($n = 3$): 0.2 to 5 ml, $\bar{x} = 4$; nighttime, middepths ($n = 3$): 2 to 13 ml, $\bar{x} = 4$; nighttime, near bottom ($n = 3$): 5 to 15 ml, $\bar{x} = 10.3$. NEW MOON–daytime, middepths ($n = 3$): 2 to 5 ml, $\bar{x} = 4$; daytime near bottom ($n = 3$): 1.2 to 5 ml, $\bar{x} = 3.7$; nighttime, middepths ($n = 3$): 3 to 13 ml, $\bar{x} = 8$; nighttime, near bottom ($n = 3$): 9 to 36 ml, $\bar{x} = 19.6$.

Thus, during the day the volumes of collections made at the middepths generally were greater than those made near the bottom, whereas the situation was reversed at night. Furthermore, volumes tended to be greater at night than during the day, with the greatest volumes of all taken near the bottom on dark nights.

Activity Patterns of the Zooplankters, Day and Night

The zooplankters are here grouped into a series of categories (Tables 1, 2),[4] most of which represent phylogenetic classes or subclasses.

Radiolarians

Based on the collections made with the plankton net (Tables 1, 2), radiolarians are consistently present in the water column during both day and night, sometimes in large numbers.

Polychaetes, Swimming

We saw polychaetes in the water column only at night. Highly motile epitokous nereids were especially prominent when they swam at middepths during reproductive periods. Polychaetes are underrepresented in the plankton collections (Tables 1, 2), however, because their mobility permitted many to evade our net.

Mollusk Larvae

Based on specimens taken in the plankton net (Tables 1, 2), mollusk veligers occur in the water column in similar numbers during both day and night.

Cladocerans

Cladocerans (Figure 5C) were consistently present in the collections during both day and night (Tables 1, 2), although they were more numerous in the daytime collections.

Ostracods

We saw ostracods in the water column at night, but never during the day. Our daytime plankton collections took only a few individuals, these close to the bottom (Table 3). At night, however, several species were consistently numerous in both middepth and near-bottom collections (Table 3). The most numerous ostracod, *Parasterope* sp. A (Figure 5H), was numerous in the surface layers of the sand during the day (Hobson and Chess in prep.), and during the middle of the night we observed and collected it concentrated at the water's surface.

Calanoid and Cyclopoid Copepods

Calanoid and cyclopoid copepods were numerous in the water column during both day and night, based on our observations in the water as well as on our collections (Tables 1, 2). Indeed, calanoids were the most numerous of all organisms larger than about 1 mm taken in the net. Calanoids and cyclopoids were collected in greater numbers at night (Table 2), but because the plankton is generally richer after dark, they represented a smaller percentage of the sample volumes at night than during the day (Table 1).

The vast majority of calanoids and cyclopoids in the collections were subadults, and some species could be recognized only as adults. Of those identified, the major calanoids were *Acartia tonsa* (Figure 5F) and *Calanus pacificus*, with others

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[4] The data in Tables 1 and 2 are from collections with the plankton net made above the open field of low benthic algae adjacent to the kelp forest. A set of day-night collections was also made within the forest (see Methods), where the fishes discussed below spend part (in some cases most) of their time. Because the data from these collections are essentially like those shown in the tables, they are not presented.

TABLE 1.—Organisms collected in the plankton net, day and night, showing size and mean percent of total volume represented by organisms in major taxonomic categories.

		Day		Night	
Organism category	Size (mm)	Middepth collections (*n* = 6)	Near-bottom collections (*n* = 6)	Middepth collections (*n* = 6)	Near-bottom collections (*n* = 6)
Radiolarians	0.1- 1.0	5.9	7.2	2.1	0.6
Polychaetes	1.0-55.0	0.3	0.3	0.3	2.1
Mollusk larvae	0.4- 0.8	0.2	0.2	0.2	0.1
Cladocerans	0.3- 1.0	11.2	1.0	0.9	0.5
Ostracods	0.5- 2.0	0.1	<0.1	0.8	1.9
Calanoids and cycloipods	0.6- 4.0	62.5	66.0	29.1	15.3
Harpacticoids	0.6- 1.0	0.2	1.3	0.6	0.8
Other copepods	1.0- 3.0	0.2	<0.1	0.1	0.1
Cirripedian larvae	0.6- 1.0	0.3	1.6	0.2	0.1
Nebaliaceans	3.0- 8.0	0.0	0.0	0.3	0.2
Mysids	1.0-12.0	0.0	0.7	39.1	47.3
Cumaceans	2.0- 5.0	0.0	0.0	2.0	3.7
Tanaids	1.0- 3.0	0.0	0.0	0.3	0.3
Isopods	1.0-10.0	0.0	0.3	1.7	2.4
Gammarideans	1.0- 5.0	0.1	0.2	10.0	14.2
Caprellids	3.0-18.0	0.0	0.0	0.4	0.8
Euphausid larvae	1.0- 3.0	0.6	1.0	0.5	0.3
Euphausid adults and juveniles	12.0-14.0	0.0	0.0	0.2	0.1
Caridean larvae	1.0- 5.0	2.0	2.3	4.8	3.9
Caridean adults and juveniles	4.0-10.0	0.0	0.0	1.0	0.7
Reptantian zoea	0.5- 4.0	0.4	0.6	0.9	0.7
Brachyuran megalops	2.0- 3.0	0.0	0.1	0.4	0.5
Bryozoan larvae	0.5- 1.0	0.7	0.6	0.7	0.5
Chaetognaths	4.0-10.0	1.3	3.4	0.6	0.3
Larvaceans[1]	1.0- 4.0	0.5	0.4	0.1	0.1
Fish eggs	0.6- 2.0	12.1	12.2	1.1	1.3
Fishes	3.0-11.0	1.6	1.9	1.5	1.2

[1] Underrepresented in collections, see text.

TABLE 2.—Organisms collected in the plankton net day and night, showing occurrence and mean number of individuals of organisms in major taxonomic categories.

	Day				Night			
	Middepth collections (*n* = 6)		Near-bottom collections (*n* = 6)		Middepth collections (*n* = 6)		Near-bottom collections (*n* = 6)	
Organism category	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Radiolarians	100	~500	100	~550	83	~3,500	83	~1,800
Polychaetes	0	0	0	0	33	<1	50	5
Mollusk larvae	33	3	33	2	50	3	50	4
Cladocerans	100	1,227	83	49	100	146	83	46
Ostracods	17	1	33	<1	100	20	100	73
Calanoids and cyclopoids	100	2,414	100	1,978	100	3,730	100	2,203
Harpacticoids	33	2	50	<1	83	23	100	41
Other copepods	17	1	17	1	17	1	17	1
Cirripedian larvae	50	6	50	30	50	5	17	2
Nebaliaceans	0	0	0	0	33	6	66	2
Mysids	0	0	50	1	100	1,100	100	1,721
Cumaceans	0	0	0	0	100	31	100	105
Tanaids	0	0	0	0	33	6	50	9
Isopods	0	0	33	3	100	23	100	49
Gammarideans	17	<1	17	3	100	436	100	2,121
Caprellids	0	0	0	0	50	4	50	15
Euphausid larvae	100	16	83	21	50	12	50	11
Euphausid adults and juveniles	0	0	0	0	17	<1	17	<1
Caridean larvae	83	31	67	45	100	200	100	220
Caridean adults and juveniles	0	0	0	0	50	25	83	10
Reptantian zoea	67	5	83	9	100	58	100	30
Brachyuran megalops	0		17	<1	50	2	67	4
Bryozoan larvae	83	71	83	12	100	117	67	21
Chaetognaths	100	35	83	31	83	7	33	4
Larvaceans[1]	67	7	50	7	17	2	17	2
Fish eggs	100	137	100	90	100	36	100	59
Fishes	67	19	50	5	83	33	83	19

[1] Underrepresented in collections, see text.

TABLE 3.—Ostracods collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Parasterope sp. A	1-2	0	0	0	0	100	10.2	83	33.8
Cycloleberis lobiancoi	1-2	0	0	0	0	67	3.5	83	18.2
Vargula americana	1-4	0	0	0	0	50	4.8	100	12.2
Philomedes sp. A	1	0	0	0	0	17	0.5	33	3.5
Unidentified species A	1	0	0	0	0	17	0.8	17	0.2
Euphilomedes carcharodonta	1-2	0	0	0	0	50	0.5	0	0
Cythereis sp.	1	0	0	17	0.2	17	0.5	0	0
Philomedes sp. B	1	0	0	0	0	17	0.5	0	0
Conchoecia sp.	1	0	0	17	0.3	0	0	0	0
Unidentified species B	2	0	0	0	0	0	0	17	0.2

present including *Candacia* spp., *Clausocalanus* sp., *Ctenocalanus* sp., *Euchaeta* sp., *Labidocera* spp., *Lucicutia* sp., *Metridia pacificus*, *Paracalanus* sp., and *Rhincalanus nasutus*. The major cyclopoid was *Coryceus* sp. (Figure 5E), but others, including *Oithona* sp., were present.

Harpacticoid Copepods

Our daytime collections took relatively few harpacticoids, all near the bottom. They were more numerous in the night collections, however, when they appeared in both middepth and near-bottom samples. One form predominated, a species of *Porcellidium*, probably undescribed, designated *Porcellidium* species A (Figure 5G). Our night middepth collections ($n = 6$) took $\bar{x} = 21.6$ specimens of this species, whereas the near-bottom collections ($n = 6$) took $\bar{x} = 37.3$. During the day *Porcellidium* species A was absent in all middepth collections ($n = 6$), but the near-bottom collections ($n = 6$) took $\bar{x} = 16$. Only one other harpacticoid was collected in daylight, a form here designated as harpacticoid species A. Our daytime middepth collections ($n = 6$) took $\bar{x} = 1.8$ specimens of this species, but it was absent in all daytime near-bottom collections, and all collections made at night. Three other forms—a second species of *Porcellidium*, and two species of *Eupelta* (all probably undescribed)—were taken only at night: a combined mean of 0.7 in the middepth collections, and a combined mean of 3.2 in near-bottom collections.

Other Copepods

No other copepods were seen in the water column, and very few were taken in the plankton net. An occasional caligoid or monstrilloid appeared in the collections, but were too few to suggest a pattern.

Cirripedian Larvae

Most of the tiny cypris larvae of the barnacles (Figure 5D) are smaller than 1 mm. Their occurrence in the collections (Tables 1, 2) was irregular, and without consistent differences between day and night, or between middepth and near-bottom samples.

Nebaliaceans

At night we occasionally observed and collected one species, probably *Nebalia pugettensis* (Figure 5J; see Smith and Carlton 1975). However, they were neither seen nor taken during the day.

Mysids

Siriella pacifica (Figure 5M) was the most widespread mysid over the study area. It remained sheltered on the sea floor and close to kelp during the day, but during late twilight moved into open water, where it spent the night (Table 4). On five evenings we noted when *S. pacifica* had first risen as much as 1 m above the bottom, and found this level attained 29 to 42 ($\bar{x} = 37.6$) min after sunset. On six mornings, the last individual 1 m above the bottom was seen 32 to 50 ($\bar{x} = 38.7$) min before sunrise. The stomach contents of 30 *S. pacifica* collected during day and night were examined: DAYTIME—of 10 (8.5-10.5 mm, $\bar{x} = 9.6$) collected amid giant kelp during midafternoon (5 from the

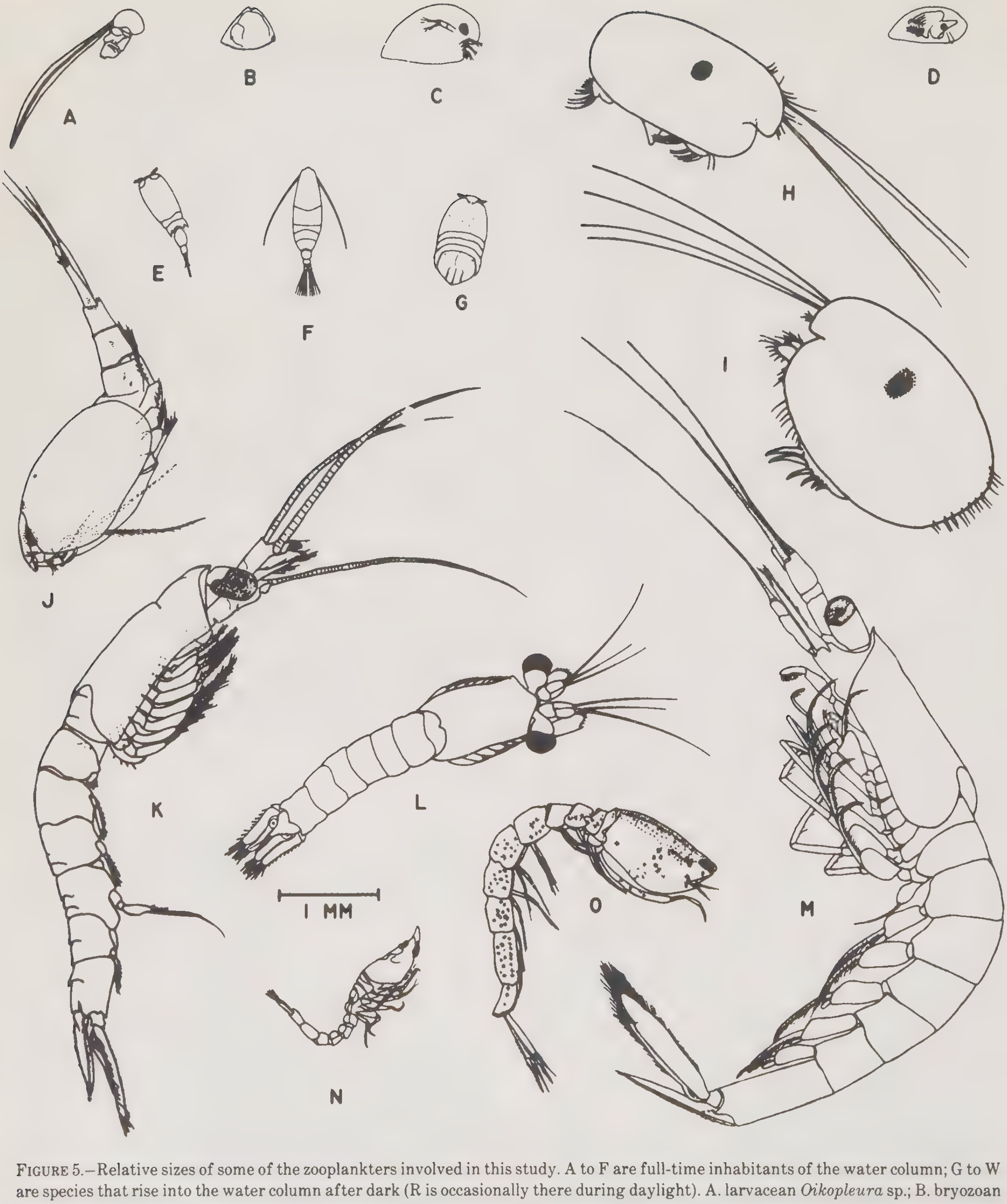
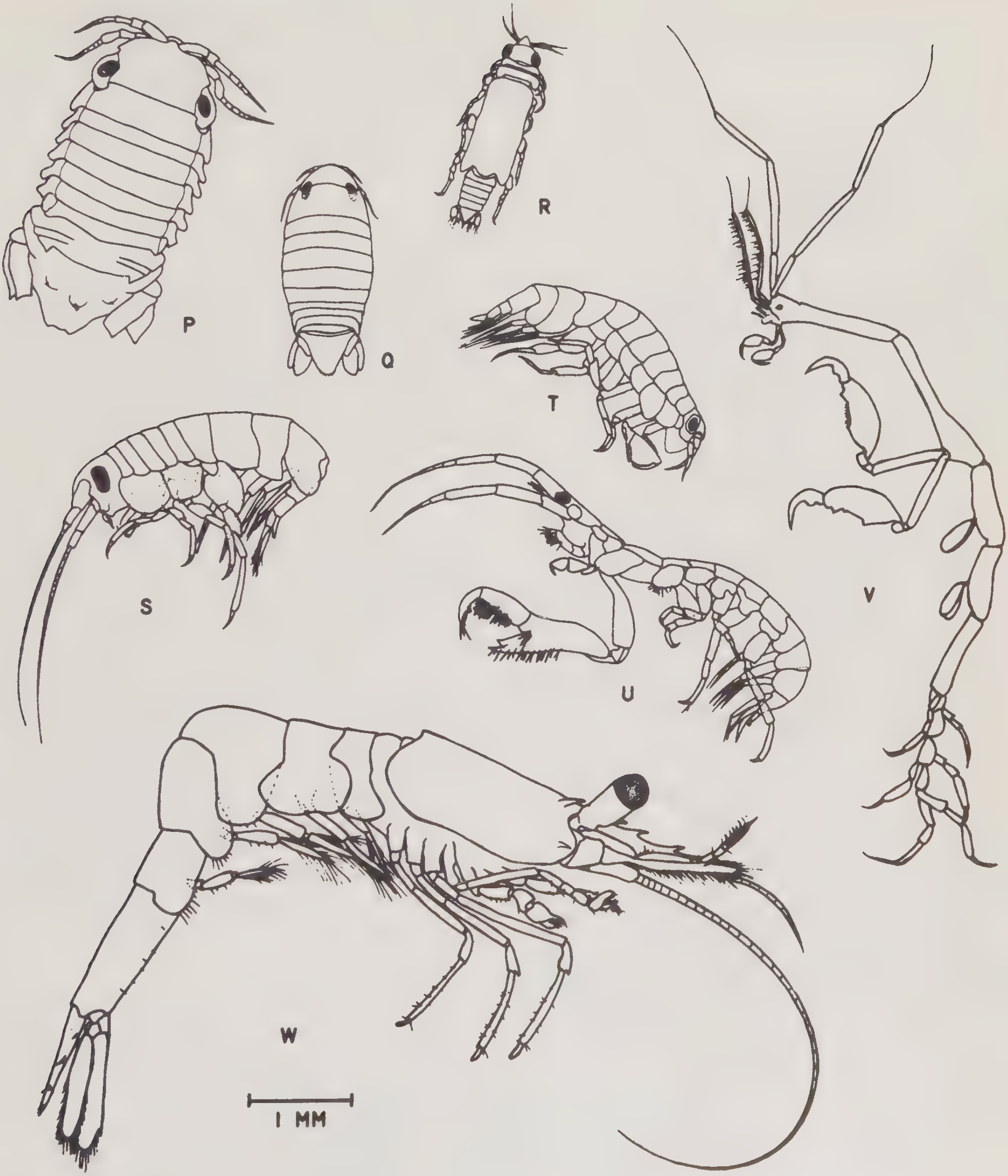


FIGURE 5.—Relative sizes of some of the zooplankters involved in this study. A to F are full-time inhabitants of the water column; G to W are species that rise into the water column after dark (R is occasionally there during daylight). A. larvacean *Oikopleura* sp.; B. bryozoan larva, cyphonautes; C. cladoceran *Evadne* sp.; D. barnacle larva, cypris; E. cyclopoid copepod *Coryceus* sp; F. calanoid copepod *Acartia tonsa*; G. harpacticoid copepod *Porcellidium* sp.; H. ostracod *Parsterope* sp. A; I. ostracod *Cycloleberis lobiancoi*; J. nebaliacean *Nebalia pugettensis*; K. mysid *Acanthomysis sculpta*; L. mysid erythropinid sp.; M. mysid *Siriella pacifica*; N. cumacean *Cumella* sp. A; O. cumacean *Cyclaspis nubila*; P. isopod *Paracercies* sp. (♀); Q. isopod *Cirolana diminuta*; R. isopod gnathiid (♀); S. gammaridean amphipod *Batea transversa*; T. gammaridean amphipod *Gitanopsis vilordes*; U. gammaridean amphipod *Ericthonias braziliensis*; V. caprellid amphipod *Caprella pilidigita*; W. caridean decapod *Hippolyte clarki*.



canopy, 5 from the lower portions of the plants), 7 were empty and 3, whose stomachs averaged 13% full, contained crustacean fragments (55% of total volume) and unidentified material. NIGHTTIME—20 individuals (7-12 mm, $\bar{x} = 10.5$) taken at middepth 2 h before first morning light had stomachs averaging 82% full, and containing crustacean fragments (100% of total volume), including copepods and cladocerans. Clearly, *S. pacifica* is a nocturnal predator.

TABLE 4.—Mysids collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Siriella pacifica	2-12	0	0	0	0	100	693.0	100	1,242.2
Erythropinid sp.	1- 6	0	0	17	5.3	100	400.3	100	468.3
Acanthomysis sculpta	4- 8	0	0	0	0	33	6.2	17	2.0
Unidentified sp.	3- 8	0	0	0	0	0	0	17	1.0

An unidentified erythropinid species (Figure 5L) behaved much like *S. pacifica*, but was seen less often. Although one daytime near-bottom collection took 32 individuals (probably the net sampled a diurnal aggregation close to the sea floor), generally the species was taken in the plankton net only at night. During the day we found it numerous amid the flocculent material that often accumulates in shallow depressions on sandy bottom (Hobson and Chess in prep.)

The predominant mysid observed and collected in the canopy of the kelp forest was *Acanthomysis sculpta* (Figure 5K), which aggregated in small openings among the kelp fronds during the day. (*Siriella pacifica* also was numerous in the kelp canopy, but not the erythropinid.) At night some *A. sculpta* moved out over the adjacent open regions sampled by our net (Table 4), but most stayed close to the kelp. The stomach contents of 20 *A. sculpta* collected during day and night were examined: DAYTIME—All 10 (8.5-11 mm, $\bar{x}$ = 10.0) collected amid the canopy of giant kelp during midafternoon contained food, with their stomachs averaging 85% full. All 10 contained plant material, apparently *Macrocystis* (69% of diet volume), while 7 contained crustacean fragments, mostly copepods, (30% of diet volume). NIGHTTIME—All 10 (8-11 mm, $\bar{x}$ = 9.6) collected in the kelp canopy 30 min before first morning light contained food, with their stomachs averaging 82% full. All 10 contained plant material, apparently *Macrocystis* (56% of diet volume), and 9 contained crustacean fragments, mostly copepods (44% of diet volume). Thus, *A. sculpta*, which does not join the other two mysid species in their mass movement into open water after dark, seems to feed on plants and animals during both day and night.

Cumaceans

Cumaceans were numerous in the water column at night, but absent there during the day. On four evenings we noted the first one to rise as much as 1 m above the bottom, and found this level attained 26 to 41 ($\bar{x}$ = 32.3) min after sunset. On four mornings we noted the last individual 1 m above the bottom, and recorded this event 37 to 50 ($\bar{x}$ = 41.3) min before sunrise. Usually we were unable to determine the species of cumaceans seen swimming in the water, but our plankton collections (Table 5) took only two species in substantial numbers: *Cumella* sp. A (Figure 5N) and *Cyclaspis nubila* (Figure 5O). Both of these species were numerous in samples of sand taken from the surface of the sea floor during the day (Hobson and Chess in prep.).

Tanaids

Tanaids were absent in the daytime collections, but one species, *Leptochelia dubia*, was collected at

TABLE 5.—Cumaceans collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Cumella sp.A	1-2	0	0	0	0	100	11.7	100	73.5
Cyclaspis nubila	2-5	0	0	0	0	67	17.8	100	29.2
Unidentified sp.	2	0	0	0	0	50	0.7	67	1.7

night. The nighttime middepth collections ($n = 6$) took $\bar{x} = 5.8$ *L. dubia*, and the nighttime near-bottom collections ($n = 6$) took $\bar{x} = 9.5$. We found this species in tubes of cemented sand grains in daytime dredge samples from sandy bottom (Hobson and Chess in prep.).

Isopods

Isopods generally were absent from the water column during the day, although the plankton collections show that at least some juvenile and female gnathiids (Figure 5R) are present. After dark, however, a number of isopods occurred in the mid-waters (Table 6). *Paracercies* spp., in particular, were numerous. Most of the specimens of *Paracercies* were juveniles or females (Figure 5P), and their identity remains uncertain. Based on the occurrence of males, *P. cordata* is by far the most numerous species of this genus in the study area, but at least one other is present.

Gammaridean Amphipods

Gammaridean amphipods were generally absent from the water column during the day, although *Gitanopsis vilordes*, which lived principally amid the dense surface canopy of the kelp forest bordering the study area (Hobson and Chess in prep.), was collected in small numbers (Table 7). At night, however, we saw gammarideans throughout the water column, and, with *Batea transversa* (Figure 5S) predominating, they were a major component of our catch in the nighttime collections (Table 7). *Batea transversa* was numerous during the day amid the low benthic algae that floors most of the study area (Hobson and Chess in prep.).

TABLE 6.—Isopods collected in the water column, day and night.

		Day				Night			
		Middepth collections ($n = 6$)		Near-bottom collections ($n = 6$)		Middepth collections ($n = 6$)		Near-bottom collections ($n = 6$)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Gnathiid juveniles	1-3	0	0	33	3	100	9.8	100	32.5
Paracerces sp.	1-3	0	0	0	0	50	11.3	67	11.2
Cirolana harfordi	2	0	0	0	0	33	1.5	17	2.0
Cirolana diminuta	3-5	0	0	0	0	17	0.2	33	0.8
Eurydice caudata	2-3	0	0	0	0	0	0	33	0.8
Excorallana kathae	10	0	0	0	0	17	0.3	17	0.2
Cirolanid sp.	3	0	0	0	0	0	0	17	0.2
Exospheroma rhomburum	3	0	0	0	0	0	0	17	0.2
Limnoria sp.	3	0	0	0	0	0	0	17	0.2

TABLE 7.—Gammaridean amphipods collected in the water column, day and night.

		Day				Night			
		Middepth collections ($n = 6$)		Near-bottom collections ($n = 6$)		Middepth collections ($n = 6$)		Near-bottom collections ($n = 6$)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Batea transversa	1-4	0	0	0	0	100	400.7	100	1,978.2
Gitanopsis vilordes	1-3	17	0.8	17	2.3	83	11.3	100	41.7
Ericthonias braziliensis	2-4	0	0	0	0	17	0.7	17	2.0
Synchelidium sp.	3	0	0	0	0	17	0.3	33	1.3
Orchomene sp.	2-4	0	0	0	0	17	0.2	50	1.3
Aoroides columbaie	3-4	0	0	0	0	0	0	33	1.3
Pleustes platypa	2	0	0	0	0	33	0.7	0	0
Ampithoe spp.	8	0	0	0	0	17	0.2	17	0.5
Podocerus cristatus	2	0	0	0	0	0	0	33	0.3
Oedocerotid sp.	3	0	0	0	0	0	0	17	0.3
Phoxocephalid sp.	2	0	0	0	0	0	0	17	0.2
Unidentified[1]	1-4	0	0	0	0	83	79.7	100	95.5

[1] Many of the unidentified specimens are juveniles, probably at least many being of the species listed above.

On four evenings we noted the first gammaridean seen as much as 1 m above the bottom, and found this level attained 27 to 39 ($\bar{x}$ = 34) min after sunset. On each occasion, individuals had been visible close among the bottom algae for about 5 min before any of them rose to the 1-m level. The final return to the sea floor at daybreak was monitored on four mornings, when the last individual was seen 1 m above the bottom 26 to 41 ($\bar{x}$ = 35) min before sunrise. Similar to the evening situation, individuals continued to be visible close above the bottom algae for an additional 5 min, or so.

To roughly determine the proportion of gammarideans that rise from the sea floor at night, we compared the amphipods in a sample of benthic algae at night, with a similar sample taken in the same place the following day (both samples, loosely packed in a 2.3-liter plastic bag, were taken immediately after plankton collections). Both samples contained 2.5 ml of animals (including other forms besides amphipods). Nevertheless, the limited data (Table 8) indicate that the numbers of some gammarideans on the algae, notably *B. transversa*, dropped sharply after dark, those of others, including *Ericthonias braziliensis* (Figure 5U), experienced a lesser decline, and those of still others remained essentially unchanged. Data from the collections (Table 7) and direct observations indicate that there were fewer amphipods on benthic algae after dark because many have risen into the water column. But the tendency to leave the sea floor clearly varies between species and in perhaps no species is it absolute. Probably at least many individuals make only short excursions into the water column.

TABLE 8.—Gammaridean amphipods collected in samples of benthic algae, day and night.

Species	No. of individuals	
	Day	Night
Species known from plankton collections		
Batea transversa	10	0
Ericthonias braziliensis	25	8
Ampithoe spp.	15	11
Aoroides columbiae	2	0
Pleustes platypa	2	0
Podocerus cristatus	1	0
Total	55	19
Species unknown from plankton collections		
Hyale nigra	10	9
Photis brevipes	2	0
Elasmopus antennatus	0	1
Heterophlias seclusus	1	0
Total	13	10
Unidentified forms[1]	26	22

[1] At least some of the unidenitfied forms probably are juveniles of the species listed above.

Caprellid Amphipods

We never saw caprellids above the bottom during the day, but saw them, though infrequently, in the water column at night. Consistent with these observations, caprellids were collected in the plankton net at night, but never during the day. The nighttime middepth collections (n = 6) took $\bar{x}$ = 3.2 *Caprella pilidigita* and $\bar{x}$ = 0.2 *C. californica*, whereas the near-bottom collections (n = 6) took $\bar{x}$ = 9.7 *C. pilidigita* and $\bar{x}$ = 5.2 *C. californica*. In addition, a single unidentified juvenile was taken in one nighttime middepth collection. Size ranges of specimens: *C. pilidigita* 4 to 18 mm, *C. californica* 6 to 10 mm, and the unidentified juvenile 3 mm. Both *C. californica* and *C. pilidigita* (Figure 5V) were at all times numerous amid the low benthic algae that floors most of the study area.

Euphausid Larvae

The calyptopis larvae of euphausids occurred regularly in both day and night collections.

Euphausid Adults and Juveniles

Euphasid adults and juveniles were neither seen nor collected in the water column during the day, but occasionally swarmed around our lights at night. The few individuals collected in the plankton net (Tables 1, 2) are of one species: *Thysanoessa spinifera*. The numbers collected, however, underrepresent the numbers we saw in the water (all of which appeared to be *T. spinifera*), probably because this relatively large, motile animal effectively evaded our net. Rather than rising from the sea floor at nightfall, as do so many other nocturnal components of the plankton discussed above, this euphausid seems to move in from deeper water. Unlike the other forms, euphausids were not taken in our extensive diurnal sampling of the benthos (Hobson and Chess in prep.).

Caridean Larvae

Based on the collections (Tables 1, 2), caridean larvae are numerous in the plankton during both day and night, but more so at night. Furthermore, there are more larger individuals in the water column after dark. We made no attempt to identify our specimens to species, but probably many are larvae of the two species discussed as adults and juveniles, below.

Caridean Adults and Juveniles

Caridean adults and juveniles were observed in the water column only at night. On the one evening that the event was noted, the first individual seen rising as much as 1 m above the bottom attained this level 39 min after sunset. Adult and juvenile carideans are absent in the daytime collections, but *Hippolyte clarki* (Figure 5W), was sometimes numerous in collections made after dark. The nighttime middepth collections ($n = 6$) took $\bar{x} = 25.2$ *H. clarki*, and the near-bottom collections ($n = 6$) took $\bar{x} = 10$. Only one other adult caridean was collected, this a single *Eualus herdmani* in a nighttime near-bottom sample. The specimens of *H. clarki* were 4 to 10 mm long, the single *E. herdmani* 12 mm. *Hippolyte clarki* is numerous during the day in the kelp forest bordering the study area, where it concentrated in the dense surface canopy and upper regions of these massive plants. At the same time *E. herdmani* predominated in the lower regions of the same plants (Hobson and Chess in prep.).

The stomach contents of 20 *H. clarki* collected during day and night were examined. DAYTIME–Of 10 (8-16 mm, $\bar{x} = 10.8$) collected from giant kelp plants during midafternoon, 4 were empty, and the other 6, whose stomachs averaged 17% full, contained only extensively macerated fragments. NIGHTTIME–Of 10 (8-17 mm, $\bar{x} = 12$) collected close to giant kelp 1 h before first morning light, 1 was empty, and the other 9, whose stomachs averaged 34% full, contained a variety of prey, some of it fresh: mollusk veligers in 4 (28% of total volume); foraminiferans in 3 (9% of total volume); shrimp larvae in 1 (11% of total volume); and extensively macerated material in 7 (52% of total volume). These limited data indicate this animal is primarily a nocturnal predator, but only a relatively few seem to swim far from algal cover.

Reptantian Zoea

Based on the collections (Tables 1, 2), zoea were consistently present in moderate numbers at all levels of the water column during both day and night, but were most numerous there after dark. Usually we failed to notice zoea in the water, but one night observed them in dense swarms close to the bottom.

Brachyuran Megalops

Our plankton collections (Tables 1, 2) indicate that brachyuran megalops were frequently present, if not numerous, in the water column at night, but only infrequently present during the day.

Bryozoan Larvae

The cyphonautes larvae of bryozoans (Figure 5B) were consistently taken in substantial numbers by middepth and near-bottom collections both day and night.

Chaetognaths

Our collections regularly took chaetognaths both day and night (Tables 1, 2), but even though these animals are relatively large, we failed to see them in the water, presumably because they are largely transparent. Chaetognaths probably were more numerous in the study area than our collection data indicate, owing to a mobility that would permit many to evade our net.

Larvaceans

We collected larvaceans in our plankton net both day and night, but only in small numbers (Tables 1, 2). It became clear that these numbers far underrepresented the numbers present, however, when we examined the gut contents of the blacksmith (recounted below). Most larvaceans in the area are less than 0.5 mm in diameter, and apparently their pliable bodies readily squeeze through the 0.333-mm mesh of our net. So we made a midday tow in the study area using a 0.25-m net with a 0.253-mm mesh. Significantly, larvaceans, most being of the genus *Oikopleura* (Figure 5A), made up 20% of the sample. There was one larvacean to about every six copepods (calanoids and cyclopoids), and they ranged from 1 to 3 mm long, with a diameter of about 0.2 to 0.5 mm. Significantly, active individuals throughout much of this size range were observed passing through a piece of 0.333-mm mesh net placed among them in a petri dish. Because these animals are transparent, and so small, we failed to see them in the water.

Fish Eggs

Fish eggs were a regular component of both middepth and near-bottom plankton collections during both day and night (Tables 1, 2). Owing to their small size and transparency, however, they went unseen by us in the water.

Fish Larvae

Fish larvae were consistently seen and collected at middepths and near the bottom both day and night (Tables 1, 2).

Activity Patterns of Planktivorous Fishes, Day and Night

Having described the zooplankters that occur in the water column during both day and night, we now consider the feeding activities of the fishes that find prey there.

Sebastes serranoides—olive rockfish

Small juveniles of this species first appeared inshore during midsummer when about 30 mm long. They remained here throughout the ensuing year, growing to about 100 to 110 mm long. Although their numbers declined sharply during the following summer, when the next crop of small juveniles arrived, many remained in the area well into a second winter, and some stayed longer. Nevertheless, few olive rockfish exceeding about 120 mm occurred in the study area. Larger individuals (to well over 200 mm) were numerous in deeper water, but were not considered in this study. Limbaugh (1955) noted: "The young appear in large schools, from May through September. The schools form behind protective reefs, in bay entrances, and in the lee of islands." Other data on this species presented by Limbaugh, and also by Quast (1968), pertain generally to individuals larger than those discussed here. The species is reported to reach 610 mm (Miller and Lea 1972).

The activity pattern of this fish changes markedly during its first year inshore. Most of the smaller juveniles are active by day and relatively inactive at night. Beginning among those about 55 mm long, however, there is a general shift toward feeding after dark. Nocturnal habits are characteristic among individuals larger than about 65 mm (to at least 120 mm—the largest considered here). This report, therefore, recognizes three size categories, and treats each separately:

1) small juveniles, which are predominantly diurnal, are those shorter than 55 mm; 2) intermediate juveniles, which represent a transition to the nocturnal mode, are those between 55 and 64 mm; and 3) large juveniles, most of which are nocturnal, are those 65 mm and longer.

SMALL JUVENILES.—During daylight, the small juveniles generally hovered in small aggregations at middepths in less than 5 m of water. In the study area they were most numerous along the shoreward margin of the kelp forest, close to rising stands of *Macrocystis* and other large algae.

The small juveniles appeared in the water column each morning, beginning about 40 min before sunrise, after a night spent sheltered under cover of algae or rocks. They occurred first as solitary individuals, but soon assembled in aggregations that were well-formed by 30 min before sunrise. Only after sunrise, however, did they feed appreciably. Then, sporatically at first, but with steadily increasing frequency, they began to snap at objects in the water indistinguishable to a human observer a few meters away.

The onset of feeding in the morning is illustrated by the decreasing incidence of empty guts in specimens collected during this period from the mid-water aggregations. Empty guts occurred in 84% of those sampled during the 40 min before sunrise (52 of 62 specimens; 42-54 mm, $\bar{x}$ = 49), in 58% of those collected during the 15 min following sunrise (7 of 12 specimens; 41-53 mm, $\bar{x}$ = 48), in 25% of those taken 15 to 30 min after sunrise (2 of 8 specimens; 45-53 mm, $\bar{x}$ = 50), and in none of those collected 30 to 60 min after sunrise (10 specimens; 41-54 mm, $\bar{x}$ = 50).

Intermittent observations throughout the day showed consistent feeding activity. The guts were full in all 11 specimens (40-51 mm, $\bar{x}$ = 45) sampled from aggregations during midafternoon. Items they had taken, combined with items taken by the 31 specimens containing food that were collected during early morning (a total sample of 42 fish), document the food habits of these small juveniles.

Prey of the 44 small juveniles that had identifiable material in their guts are listed below in order of their rank as prey. (The same format is used in presenting the gut contents of the other fish species, below.) In this list, the major numbered categories are the same as those in which the zooplankters are organized in Tables 1 and 2 and in the text above. The few additional major categories include various nonplanktonic organisms that some of these fishes had taken in small numbers. Listed under each major category, according to rank within that category, are the species and species groups that are the actual prey of the fish. Following most entries throughout the listing are sets of three values in parentheses; these values relate certain characteristics of the entry to the food habits of the fish. (The values were derived from calculations based only on fish that contained identifiable material. Fish with empty guts or containing only unidentifiable material were not considered.) The first value in parentheses is the percent of fish that contained the item(s); the second value is the mean number of individuals of the item(s) that were taken, and the third value is the mean percent of the diet volume represented by the item(s). Rank as prey was determined by a ranking index, which is not shown, but which is the product of the first and third values in parentheses.

Following the above format, the prey organisms are:

1. CALANOID AND CYCLOPOID COPEPODS (83: 44.4: 59.5)
   calanoids, including *Acartia tonsa* and *Labidocera* sp. (81: 40.3: 54.9); cyclopoids, including *Corycaeus* sp. (38: 4.1: 4.6).
2. GAMMARIDEAN AMPHIPODS (29: 0.4: 11.4)
   Batea transversa (18: 0.3: 7.6); unidentified fragments (11: 0.1: 3.8).
3. CARIDEAN LARVAE (20: 0.4: 3.2)
   unidentified species.
4. MYSIDS (11: 0.3: 4.5)
   Acanthomysis sculpta (3: 0.1: 2.0); erythropinid sp. (3: 0.1: 0.5); unidentified fragments (7: 0.1: 2.0).
5. CLADOCERANS (20: 1.1: 2.4)
   Evadne sp.
6. OTHER COPEPODS (18: 0.3: 2.2)
   unidentified monstrilloids.
7. EUPHAUSID ADULTS AND JUVENILES (11: 0.1: 1.3)
   unidentified fragments.
8. BRACHYURAN MEGALOPS (5: 0.1: 4.8)
   unidentified.
9. HARPACTICOID COPEPODS (18: 0.4: 1.2)
   harpacticoid sp. A (7: 0.1: 0.7); *Porcellidium* sp. B (5: 0.1: 0.2); *Porcellidium* sp. A (2: 0.1: 0.1); unidentified fragments (5: 0.1: 0.2).
10. TANAIDS (10: 0.2: 2.4)
    Leptochelia dubia (7: 0.1: 1.2); unidentified fragments (3: 0.1: 1.2).
11. REPTANTIAN ZOEA (11: 0.1: 1.3)
    unidentified.
12. FISHES (5: 0.2: 2.0)
    unidentified larvae.
13. ISOPODS (2: <0.1: 1.1)
    Paracercies sp.
14. GASTROPODS (2: 0.4: 0.5)
    Tricolia sp.
15. EUPHAUSID LARVAE (2: <0.1: 0.1)
    calyptopsis.
16. CIRRIPEDIAN LARVAE (5:<0.1: <0.1)
    cypris.
17. BRYOZOAN LARVAE (2: <0.1: <0.1)
    cyphonautes.

Small juveniles took calanoid copepods as their major prey from the time they began feeding at sunrise until they ceased feeding at the end of the day. In 10 specimens collected during May and June (the only times for which calanoids in this material were identified to species), about 22% of the calanoids were *Acartia tonsa*, and although the rest remained unidentified (except for a single specimen of *Labidocera* sp.), many probably were immature individuals of this same species.

A number of the prey listed above occurred only in specimens collected during early morning. These are: the gamaridean amphipods, the tanaids, the euphausids, the lone isopod, the megalops, and all mysids except those in one individual (see below). Most of these items were extensively digested, in sharp contrast to the freshness of the calanoids and other food materials in the early-morning specimens. Clearly, they had been in the guts for some time, probably since the previous night. Nevertheless, judging from the empty guts in most individuals of this size at daybreak it would seem that nocturnal feeding is insignificant.

Only later than about 30 min after sunrise did the olive rockfish begin taking *Evadne* sp., but this cladoceran then became a consistant component of the diet for the rest of the day. *Evadne* is slightly smaller and more transparent than the other prey organisms, and to capture it the rockfish may need more light. The only mysid taken during the day was *Acanthomysis sculpta*, of which two individuals that appeared recently ingested were found in one olive rockfish during midafternoon.

INTERMEDIATE JUVENILES.—Individuals between about 55 and 65 mm long were highly inconsistent in so far as whether they fed by day or by night (many did both). The nocturnal situation among intermediate individuals is represented by 18 specimens (55-63 mm, $\bar{x} = 58$) collected before sunrise from open water during the hour before first morning light, and also from developing aggregations of juveniles more than 30 min before sunrise. Of these, 13 (72%) were full of prey in varying stages of digestion, demonstrating nocturnal feeding, whereas 5 (28%) were empty, indicating they had been inactive that night. All the empty fish were from the developing aggregations, but many of those containing food were also taken from those aggregations. Items taken at night by the 13 intermediate juveniles containing food were as follows, with the format being that used for the small juveniles, above.

1. GAMMARIDEAN AMPHIPODS (69: 2.9: 28.5)
   including *Batea transversa* and *Ericthonias braziliensis.*
2. CUMACEANS (54: 2.7: 26.3)
   Cyclaspis nubila (46: 2.6: 26.1); *Cumella* sp. A (8: 0.1: 0.2).
3. MYSIDS (38: ?: 16.2)
   Siriella pacifica (23: 0.3: 13.1); unidentified fragments (15: ?: 3.1).
4. FISHES (15: 7.1: 5.4)
   unidentified larvae.
5. CAPRELLID AMPHIPODS (8: 0.5: 6.2)
   Caprella pilidigita.
6. POLYCHAETES, SWIMMING (8: ?: 5.0)
   unidentified fragments.
7. OSTRACODS (8: 0.1: 0.8)
   Parasterope sp. A
8. BRACHYURAN MEGALOPS (8: 0.5: 0.4)
   unidentified.

The diurnal feeding situation, as well as the changeover from day to night, is represented by 12 individuals (55-62 mm, $\bar{x} = 58$), all with full guts, collected from among feeding aggregations of small juveniles within 1 h after sunrise. Almost all the food items in this sample were either fresh or well-digested–there was little in between. Presumably, the fresh items were those that had been taken after feeding began within the previous hour, whereas the extensively damaged items had been taken during the night before. (One would expect specimens taken as early in the morning as these to contain evidence of any nocturnal feeding they might have done, and this proved true here.) Seven of the 12 individuals sampled contained both fresh and well-digested material in large numbers, always with the fresh items forward in the gut (often in the esophagus), and the well-digested items well back in the posterior region. Clearly, these individuals had fed substantially during both day and night (a conclusion strengthened by the kinds of prey among the fresh and well-digested segments of the diet, see below). Three of the other five specimens contained only fresh items, indicating diurnal feeding exclusively, whereas two contained just well-digested material, indicating only nocturnal feeding. Food items in this material are identified below, but with fresh items listed separately from well-digested items.

FRESH ITEMS

1. CALANOID AND CYCLOPOID COPEPODS (83: 65.9: 47.8)
   calanoids (83: 65.7: 47.5); cyclopoids (17: 0.2: 0.3).
2. CLADOCERANS (33: 0.8: 0.8)
   Evadne sp.
3. OSTRACODS (8: 0.1: 1.7)
   Cycloleberis lobiancoi.
4. OTHER COPEPODS (8: 0.1: 0.4)
   monstrilloids.
5. ISOPODS (8: 0.1: 0.4)
   gnathiid juveniles.
6. HARPACTICOID COPEPODS (8: 0.2: 0.2)
   Porcellidium sp. A.
7. CARIDEAN LARVAE (8: 0.1: 0.3)
   unidentified.

WELL-DIGESTED ITEMS

1. GAMMARIDEAN AMPHIPODS (50: 1.3: 1.1)
   including *Batea transversa.*
2. CARIDEAN LARVAE (33: 2.2: 12.9)
   unidentified.
3. EUPHAUSID ADULTS AND JUVENILES (17: 0.7: 10.7)
   unidentified fragments.
4. FISHES (17: 1.0: 9.2)
   unidentified larvae.
5. REPTANTIAN ZOEA (17: 0.3: 2.0)
   unidentified.
6. BRACHYURAN MEGALOPS (8: 0.3: 1.3)
   unidentified.
7. INSECTS (8: 0.1: 0.8)
   unidentified.
8. CAPRELLID AMPHIPODS (8: 0.1: 0.4)
   unidentified.

The fresh items apparently represent diurnal feeding, the well-digested items nocturnal feeding. Thus, among individuals within the intermediate size range there obviously are many that forage during both day and night.

LARGE JUVENILES.–During the day, olive rockfish more than about 65 mm long generally hovered in small aggregations low in the water column beneath the kelp canopy within the seaward part of the forest (Figure 6). Aggregations composed of relatively large individuals (exceeding a length of about 100 mm) sometimes hovered above others of the same size seated on the rocks below.

In contrast to the small individuals described above, large juveniles generally showed no sign of feeding during the day, an observation supported

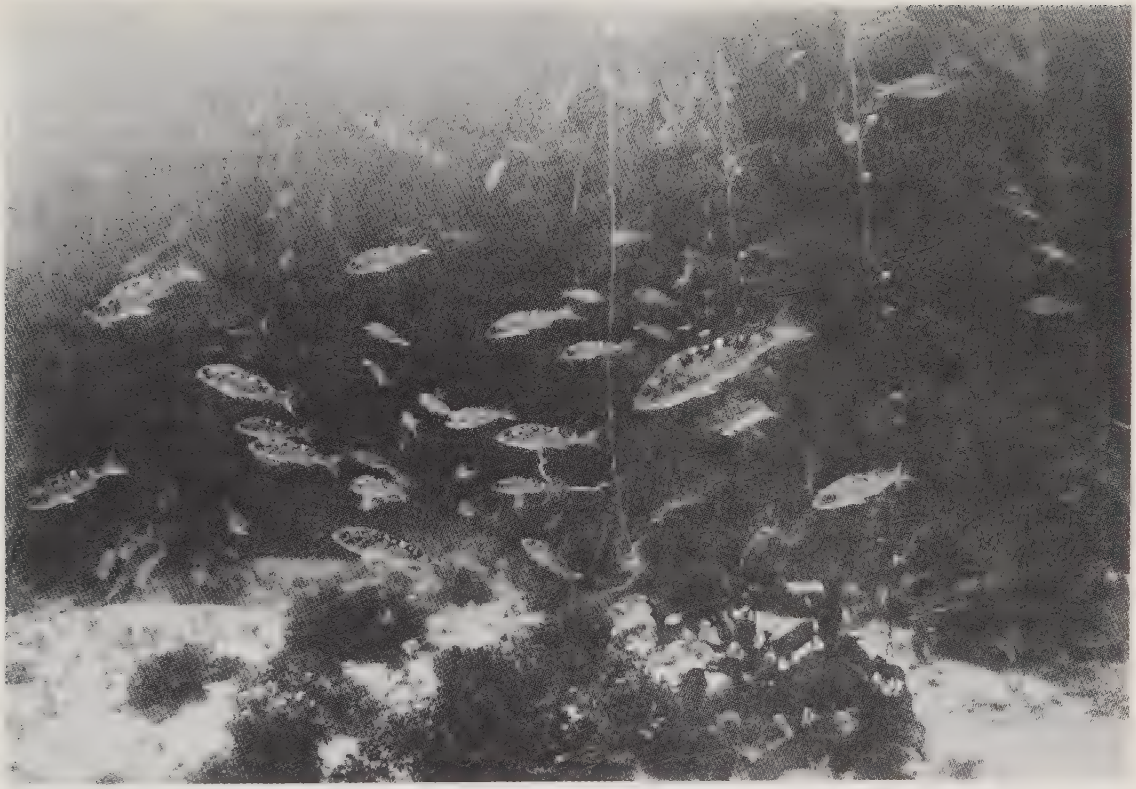


FIGURE 6.—A daytime aggregation of large juvenile olive rockfish, *Sebastes serranoides*. Many nocturnal fishes spend the day in quiet schools.

by examination of gut contents. Of 42 specimens (65-120 mm, $\bar{x} = 91$) collected from aggregations during midafternoon, 28 (67%) had empty guts, and 8 (19%) contained only well-digested fragments. Six (14%), however, contained relatively fresh prey probably captured earlier that day: the mysid *Acanthomysis sculpta* (50: 15.7: 32.5); the caridean shrimps *Hippolyte clarki* (50: 0.5: 14.2) and *Eualus herdmani* (17: 0.2: 5.2); the cladoceran *Evadne* sp. (17: 4.3: 10.0); calanoid copepods (17: 1.5: 5.2); euphausid larvae, calyptopis stage (17: 0.5: 1.6); and harpacticoid copepod *Porcellidium* sp. A (17: 0.2: 0.1). Also present were extensively digested fragments of cumaceans, tanaids, euphausids, and mysids (33: ?: 20.5) that probably had been taken the night before (a judgment influenced by knowledge of nocturnal food habits, defined below). All of the cladocerans, calanoids, and euphausid larvae among this material constituted the entire gut contents of one 82-mm individual, and the contents suggest a mode of feeding like that of the small juveniles above.

Beginning about 20 min after sunset, large juveniles began leaving the sites of their daytime aggregations. They moved away from the kelp forest, and dispersed over the adjacent field of *Dictyopteris*. Many of them rose into the upper part of the water column, but most remained within 5 m of the sea floor. They remained in these positions throughout the night, often assuming a tail-down attitude, now and then darting a few centimeters forward and snapping at objects in the dark water. The few that remained in the kelp forest usually hovered high in the water column beneath sizeable breaks in the kelp canopy. They began returning to the forest at first morning light, and by 30 min before sunrise were back in their daytime aggregations.

Clearly, olive rockfish of this size feed chiefly at night. This conclusion is supported by study of gut contents from 72 specimens (65-157 mm, $\bar{x} = 85$) collected in this area at night—later than 4 h after sunset, and before first morning light. Only two of these (less than 3%) had an empty gut, a contrast to the high incidence of empty guts (67%) among specimens collected during the afternoon. More significant, the gut of all 70 other specimens contained many fresh items, all organisms present in the water column after dark.

Major categories of prey with included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (90: 16.9: 43.9)
   Batea transversa 76: 8.5: 21.9); *Ericthonias braziliensis* (19: 1.1: 2.6); *Ampithoe* spp. (20: 1.3: 2.4); *Photis brevipes* (14: 1.2: 0.8); *Ampelisca* sp. (3:<0.1: 1.6); *Synchelidium* sp. (9: 0.1: 0.6); *Aoroides columbiae* (9: 0.1: 0.4); *Hyale nigra* (3: 0.1: 0.3); *Monoculoides* sp. (3: 0.3: 0.2); *Podocerus cristatus* (4: <0.1: 0.1); phoxocephalid sp. (3: <0.1: 0.1); lysianassid spp. (1: <0.1: 0.1); *Paraphoxus* sp. (1:<0.1: 0.1); *Pleustes platypa* (1: <0.1: 0.1); unidentified gammarideans, including unknown forms and those unrecognized due to damage (73: 3.9: 12.6).
2. MYSIDS (69: 2.7: 12.5)
   Siriella pacifica (47: 1.7: 9.2); erythropinid sp. (40: 0.9: 3.1); *Acanthomysis sculpta* (3: <0.1: 0.2).
3. CUMACEANS (57: 4.9: 8.4)
   Cyclaspis nubila (37: 4.1: 7.2); *Cumella* sp. (40: 0.8: 1.1); unidentified (3: <0.1: 0.1).
4. POLYCHAETES, SWIMMING (36: 0.5: 8.6)
   at least most of them nereids.
5. CAPRELLID AMPHIPODS (36: 1.4: 7.0)
   Caprella pilidigita (24: 0.8: 4.2); *C. californica* (19: 0.5: 2.6); *C. brevirostis* (1: <0.1: 0.1); unidentified species (1: 0.1: 0.1).
6. OSTRACODS (43: 1.6: 3.8)
   Parasterope sp. A (37: 1.0: 2.9); *Vargula americana* (9: 0.3: 0.5); *Philomedes* sp. (4: 0.1: 0.2); *Cycloleberis lobiancoi* (3: <0.1: 0.1); unidentified (1: <0.1: 0.1).
7. ISOPODS (39: 1.7: 3.3)
   Paracercies sp. (27: 0.8: 2.1); gnathiid juveniles and females (21: 0.8: 0.8); *Idotea* spp. (4: 0.1: 0.1); *Cirolana diminuta* (3: <0.1: <0.1); *Limnoria lignorum* (1: <0.1: 0.1); *Excorallana kathae* (1: <0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (24: 0.4: 4.1)
   Hippolyte clarki (20: 0.2: 2.2); *Eualus herdmani* (6: 0.2: 1.9).
9. TANAIDS (26: 0.5: 1.2)
   Leptochelia dubia (25: 0.4: 1.0); unidentified (4: 0.1: 0.2).
10. EUPHAUSID ADULTS AND JUVENILES (7: 0.1: 2.0)
    Thysanoessa sp. (1: <0.1: 0.7); unidentified (6: 0.1: 1.3).
11. FISHES (9: <0.1: 1.6)
    unidentified larvae.
12. BRACHYURAN MEGALOPS (10: 0.2: 0.7)
    unidentified.
13. CARIDEAN LARVAE (9: 4.0: 0.6)
    unidentified.
14. HARPACTICOID COPEPODS (13: 0.2: 0.2)
    Porcellidium sp. A.
15. REPTANTIAN ZOEA (6: 0.6: 0.4)
    unidentified.
16. CALANOID AND CYCLOPOID COPEPODS (4: <0.1: 0.2)
    unidentified cyclopoids.
17. OTHER COPEPODS (1: <0.1: 0.1)
    unidentified caligoids.
18. NEBALIACEANS (1: <0.1: <0.1)
    Nebalia pugettensis.

Sebastes atrovirens—kelp rockfish

The kelp rockfish, which may attain a length of 425 mm (Miller and Lea 1972), was the most numerous adult scorpaenid in the study area. During the day, a few individuals hovered above the sea floor in shadow under the kelp canopy, but most spent the daytime seated on rocky substrata within the forest—quiet but alert. At night this fish generally hovered in mid-water close to the rising kelp stipes (Figure 7), and often amid the kelp canopy, near the water's surface. Occasionally at night it hovered in open water close along the seaward margin of the forest. Differences in activities between day and night have gone unnoted in previous reports of this species. Limbaugh (1955) reported that it lives in the lower levels of the kelp and among the rocks, and feeds on "crustaceans and small fish." Quast (1968), on the other hand, reported that it ranges all the way from the bottom to the kelp canopy and apparently utilizes "all available foods in these regions."

Of 29 specimens (89-240 mm, $\bar{x} = 175$) collected for study of food habits, all 6 (100%) taken during midafternoon were empty, whereas only 3 of 23 (13%) taken at night (more than 4 h after sunset) were empty. Clearly, this fish is predominantly a nocturnal feeder. Quast (1968) noted that many of the kelp rockfish he examined had an empty stomach but did not suggest nocturnal feeding. He noted that his specimens "appeared quite thin," and though recognizing this may be a natural condition, thought perhaps "the high frequencies of empty stomachs and the broad variety of food items found may indicate malnutrition." The kelp rockfish of our study area, we have noted, often have deeply concaved bellies during the day, which we assume is due to the emptiness of their guts at this time.

Almost all food materials taken by this fish were from the water column. The major food categories, which included species and species groups, are listed below in order of their rank as prey.

1. MYSIDS (90: 22.3: 39.5)
   Acanthomysis sculpta (60: 18.3: 30.1); *Siriella pacifica* (65: 3.6: 9.2); erythropinid sp. (15: 0.4: 0.2).
2. CARIDEAN ADULTS AND JUVENILES (85: 7.0: 16.2)
   Hippolyte clarki (65: 4.4: 10.0); *Eualus herdmani* (40: 2.6: 6.2).
3. GAMMARIDEAN AMPHIPODS (95: 13.8: 13.7)
   Batea transversa (95: 9.3: 9.5); lysianassid spp. (50: 1.2: 1.1); *Ampelisca* sp. (10: 1.4: 1.3); *Pleustes platypa* (25: 0.3: 0.3); *Podocerus cristatus* (5: 0.1: 0.2); *Ampithoe tea* (5: 0.1: 0.2);

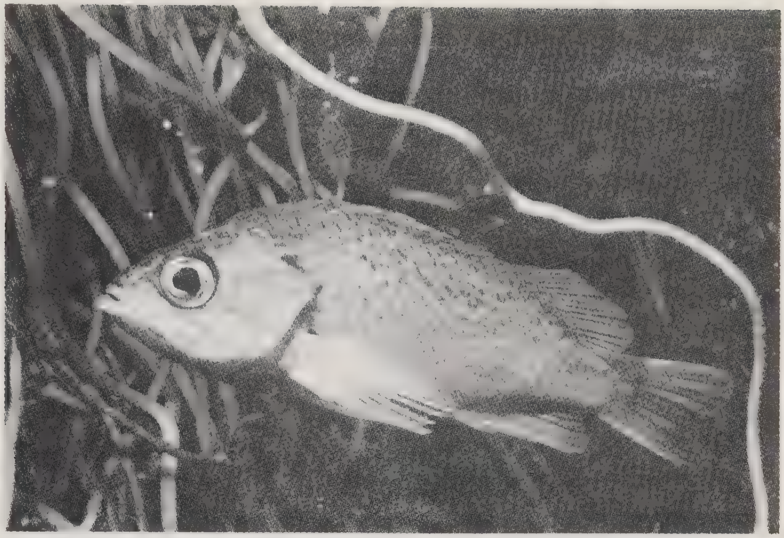


FIGURE 7.—A solitary kelp rockfish, *Sebastes atrovirens*, close to rising stipes of a giant kelp plant at night.

Aoroides columbiae (15: 0.2: 0.1); *Hyale nigra* (5: 0.1: 0.1); *Ericthonias braziliensis* (5: 0.2: 0.1); unidentified (40: 0.9: 0.8).

4. ISOPODS (75: 3.7: 14.3)
   Paracercies sp. (75: 3.3: 11.8); *Pentidotea resecata* (5: 0.1: 1.8); gnathiid juveniles (10: 0.1: 0.3); *Cirolana harfordi* (10: <0.1: 0.2); *Idotea rectolineata* (5: <0.1: 0.2).
5. POLYCHAETES, SWIMMING (20: 0.3: 7.1)
   unidentified, but only certain epitokous nereids were significant, these being prominent in the guts on nights when they swam in mid-water.
6. BRACHYURAN ADULTS (10: 0.1: 4.2)
   all *Pugettia producta*.
7. OSTRACODS (30: 0.5: 0.9)
   Cycloleberis lobiancoi (20: 0.2: 0.5); *Vargula americana* (10: 0.2: 0.3); *Parasterope* sp. A (5: 0.1: 0.1).
8. FISHES (15: 0.1: 1.2)
   larvae (10: 0.1: 0.8); scales (5: ?: 0.4).
9. NEBALIACEANS (5: 0.1: 1.1)
   Nebalia pugettensis.
10. CUMACEANS (5: 0.3: 0.7)
    all *Cyclaspis nubila*.
11. GASTROPODS (5: 0.1: 0.1)
    Lacuna unifasciata.
12. EUPHAUSID ADULTS AND JUVENILES (5: 0.1: 0.1)
    unidentified.

Xenistius californiensis—salema

We never saw salema in the study area during the day, but at night frequently encountered solitary individuals (Figure 8), or loosely spaced groups of four to six. Usually they swam high in the mid-waters above the open fields of *Dictyopteris* within 10 m of the forest. Their first appearance in the evening consistently occurred about 40 min after sunset, apparently after they had come from some distance away. The relatively few times we saw this species in daylight (always more than 400 m from the study area), it swam in schools of more than 50 individuals, closely spaced and seemingly inactive, at middepths within the forest. Reportedly this fish reaches 255 mm (Miller and Lea 1972).

Fresh material filled the stomachs of all five specimens (163-180 mm, $\bar{x}$ = 170) collected for study of food habits. They were taken at night, more than 3 h after sunset, and before daybreak, and so nocturnal feeding is apparent. All three

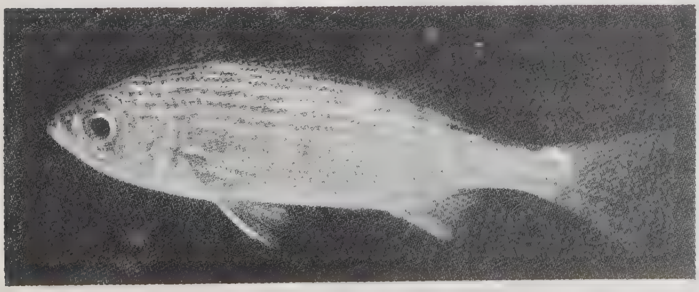


FIGURE 8.—A solitary salema, *Xenistius californiensis*, swims above the sea floor at night.

taken before midnight had their intestines empty; this, considering also the inactive appearance of those in diurnal schools, suggests lack of daytime feeding. Quast (1968) reported a high incidence of empty stomachs in specimens that he collected during the day, but did not relate this to nocturnal feeding.

All food material in the guts of specimens collected during this study are organisms that occured in the water column. Major categories of prey, which included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (100: 44.8: 38.2)
   Batea transversa (100: 26.0: 30.0); *Ampithoe plumulosa* (20: 5.2: 3.0); *Ericthonias braziliensis* (20: 2.0: 1.0); lysianassid spp. (20: 0.2: 0.4); *Gitanopsis vilordes* (20: 0.2: 0.2); *Ampithoe* spp. (20: 4.0: 1.0); unidentified species (60: 7.2: 2.6).
2. MYSIDS (100: 22.0: 28.0)
   Siriella pacifiica (100: 20.2: 26.8); erythropinid sp. (60: 1.8: 1.2).
3. POLYCHAETES, SWIMMING (40: ?: 20.0)
   unidentified species, mostly epitokus nereids.
4. CUMACEANS (60: 2.0: 2.6)
   Cyclaspis nubila (60: 1.6: 2.2); unidentified juveniles (20: 0.4: 0.4).
5. CAPRELLID AMPHIPODS (40: 5.6: 3.0)
   Caprella pilidigita (40: 4.4: 1.8); *C. californica* (40: 1.2: 1.2).
6. OSTRACODS (80: 2.2: 1.0)
   Parasterope sp. A (60: 1.2: 0.6); *Cycloleberis lobiancoi* (20: 0.6: 0.2); *Vargula americana* (20: 0.4: 0.2).
7. NEBALIACEANS (20: 1.0: 3.0)
   Nebalia pugettensis.
8. ISOPODS (40: 2.4: 1.2)
   Cirolana harfordi (20: 0.8: 0.4); *Paracercies* sp. (20: 1.0: 0.2); *Excorallana kathae* (20: 0.4: 0.2); gnathiid juveniles (20: 0.2: 0.4).
9. FISHES (20: ?: 1.8)
   scales.
10. CARIDEAN LARVAE (20: 1.2: 0.6)
    unidentified.
11. CARIDEAN ADULTS AND JUVENILES (20: 1.2: 0.6)
    unidentified.
12. REPTANTIAN ZOEA (20: 3.6: 0.4)
    unidentified.
13. CALANOID AND CYCLOPOID COPEPODS (20: 0.2: 0.2)
    calanoid, *Labidocera* sp.

This list indicates a diet much like that of salema collected from a kelp bed near La Jolla by Quast (1968), although Quast questioned the validity of his data because of the collecting methods used.

Seriphus politus—queenfish

The queenfish, which can grow to 304 mm (Miller and Lea 1972), consistently appeared in the study area about 40 min after sunset and remained active there throughout the night. Generally, solitary individuals, or loosely spaced groups of two to six swam several meters above the sea floor, usually close to the seaward edge of the kelp forest, but frequently above the open fields of *Dictyopteris*. Then, shortly after first morning light, 40 to 50 min before sunrise, they abruptly left the area.

During the day queenfish hover in dense, relatively inactive schools close to shore (Figure 9), but we have not seen them within 1.5 km of the study site in daylight. Limbaugh (1955), presumably assessing the daytime situation, stated:

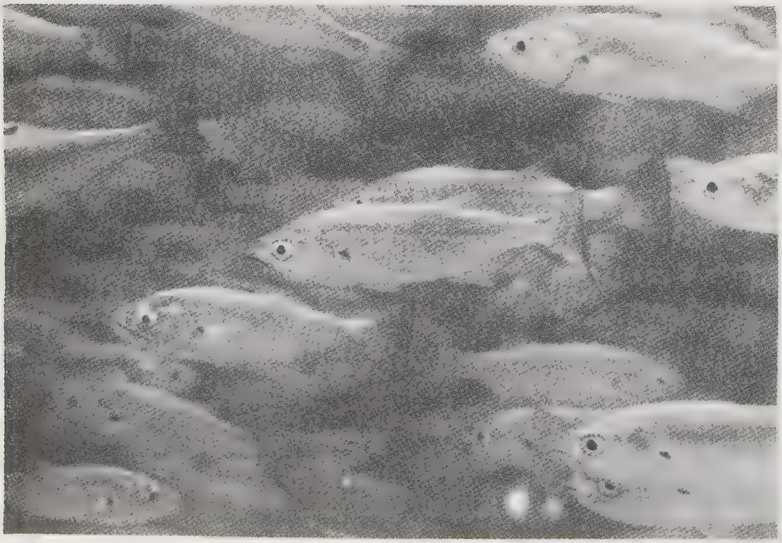


FIGURE 9.–A daytime aggregation of queenfish, *Seriphus politus*.

"Queenfish school in tightly packed aggregations over sandy bottom."

Four of five individuals (124-171 mm, $\bar{x}$ = 148) collected shortly after they had arrived in the study area at nightfall had an empty gut, and the fifth contained just a single freshly ingested shrimp (unidentified). We conclude that these individuals had passed the previous day without feeding. The evidence further suggests they do not feed while en route from daytime schooling sites to their feeding ground in the study area.

All 31 specimens (114-193 mm, $\bar{x}$ = 151) sampled in the study area at night, later than 3 h after sunset and before first morning light, had material in their guts—much of it fresh. All prey belonged to groups known to occur in the water column. Limbaugh (1955) reported that this species feeds on "small free-swimming crustaceans and fish." Below are ranked the species and species groups taken as prey by this fish.

1. MYSIDS (84: 22.5: 44.7)
   Siriella pacifica (84: 21.0: 39.6); *Acanthomysis sculpta* (52: 1.4: 5.0); erythropinid sp. (6: 0.1:<0.1).
2. GAMMARIDEAN AMPHIPODS (89: 16.0: 21.6)
   Batea transversa (84: 15.6: 20.2); *Ampelisca* sp. (9: 0.2: 0.3); lysianassid spp. (6: 0.1: 0.2); *Ampithoe* sp. (3: 0.1: 0.1); unidentified (3: <0.1: 0.8).
3. POLYCHAETES, SWIMMING (31: 0.8: 21.8)
   Epitokous nereids (22: 0.7: 18.4); unidentified (9: <0.1: 3.4).
4. CARIDEAN ADULTS AND JUVENILES (44: 0.7: 5.9)
   Eualus herdmani (28: 0.4: 2.0); *Hippolyte clarki* (19: 0.3: 2.0); unidentified (3: <0.1: 1.9).
5. ISOPODS (34: 0.7: 3.6)
   Paracercies sp. (22: 0.5: 1.7); gnathiid juveniles (13: 0.1: 0.2); *Limnoria* sp. (3: 0.1: 1.1); *Excorallana kathae* (3: <0.1: 0.5); *Cirolana harfordi* (3: <0.1: 0.1).
6. FISHES (6: 0.6: 1.4)
   scales.
7. NEBALIACEANS (6: 0.1: 0.2)
   Nebalia pugettensis.
8. OSTRACODS (13: 0.3: 0.2)
   Vargula americana (6: 0.1: <0.1); *Cycloeberis lobiancoi* (3: 0.1: <0.1); *Parasterope* sp. A (3: 0.1: <0.1).
9. CARIDEAN LARVAE (3: <0.1: 0.3)
   unidentified.
10. BRACHYURAN MEGALOPS (3: <0.1: 0.2)
    unidentified.
11. EUPHAUSID ADULTS AND JUVENILES (3: <0.1: <0.1)
    unidentified.
12. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.

A single small juvenile queenfish, 38 mm long, was collected on 2 November shortly before first morning light as it swam alone close over the sand. Its full gut contained mysid *Siriella pacifica*, gammaridean amphipod *Batea transversa*, and isopod *Limnoria* sp. All of these forms are also prey of larger queenfish, but those taken by this small individual were less than half the size of prey routinely taken by the larger fish.

Material that we collected at La Jolla in 1971 included some information on smaller juveniles. Ten individuals (10-27 mm, $\bar{x}$ = 19) were collected on the same day during the hour before first morning light—all from the stomachs of larger individuals of their own species. Of these, only the two largest, 23 and 27 mm, contained prey of the types taken by larger conspecifics: mysids and gammaridean amphipods constituted 99% of the diet of these two, with calanoid copepods representing the remainder. In contrast, calanoid copepods were the major prey of the seven smaller individuals (in six, 80% of the total diet). Fish larvae (in one, 11% of the total diet), and cladocerans (in one, 9% of the total diet), constituted the rest. These limited data indicate that the queenfish, like the olive rockfish above, changes as it grows from a diet of copepods to one of mysids and other plankters that appear after dark. The queenfish, however, seems to make the change at a smaller size, perhaps because it has a larger mouth. Moreover, the data fail to show that the queenfish, like the olive rockfish, feeds by day when subsisting on copepods.

Hyperprosopon argenteum— walleye surfperch

The walleye surfperch, which can grow to 304 mm (Miller and Lea 1972), consistently schooled during the day in about 2 to 5 m of water over sand at the edge of the forest at the head of Fishermen's Cove. Usually these schools included 20 to more than 100 closely spaced individuals. Members of these schools appeared inactive, an impression supported by the eight empty guts found in nine individuals (115-173 mm, $\bar{x}$ = 140) taken during midafternoon (and the ninth contained only well-digested fragments). Presumably describing the daytime situation throughout southern California, Limbaugh (1955) stated: "They school in an aggregate cloud . . . over sand patches among rocks."

The schools dispersed at nightfall, and many individuals spread along the seaward edge of the forest at the perimeters of the cove. They swam individually (Figure 10) or in small groups 1 to 3 m above the bottom, usually over sand within a few meters of, but sometimes within, the forest. Of the 35 (60-151 mm, $\bar{x}$ = 111) collected in the study area between 4 h after sunset and daybreak, only one

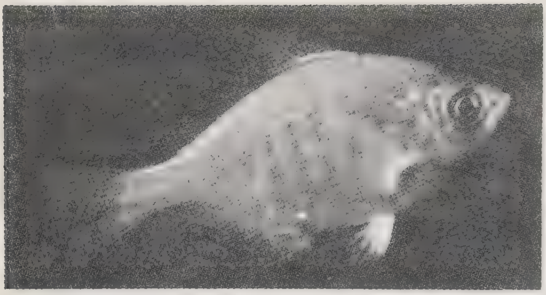


FIGURE 10.—A solitary walleye surfperch, *Hyperprosopon argenteum*, swims in the water column at night.

was empty; the rest were full of prey, much of it fresh.

Clearly, this is a nocturnal fish. Those seen in the study area at night, however, tended to be smaller on the average than those seen in the diurnal schools, suggesting that the larger fish might range farther away. All prey in the 34 individuals containing identifiable material were organisms that occur in the water column, as listed below.

1. GAMMARIDEAN AMPHIPODS (100: 63.6: 47.0)
   Batea transversa (85: 39.8: 24.2); *Ampithoe* spp. (41: 3.3: 3.8); *Hyale nigra* (9: 2.8: 2.9); *Ericthonias braziliensis* (15: 0.5: 1.1); *Ampelisca* sp. (15: 0.6: 1.0); *Synchelidium* sp. (24: 0.4: 0.3); lysianassid spp. (15: 0.6: 0.2); *Heterophilias seclusus* (6: 0.1: 0.1); *Photis* sp. (3: <0.1: 0.1); *Paraphoxus* sp. (3: <0.1: <0.1); *Aoroides columbiae* (3: <0.1: 0.1); unidentified (91: 15.4: 13.2).
2. CUMACEANS (85: 52.9: 25.2)
   Cyclaspis nubila (76: 51.2: 24.8); *Cumella* sp. A (18: 1.7: 0.4).
3. ISOPODS (72: 21.1: 10.2)
   Paracercies sp. (65: 19.5: 7.6); gnathiid juveniles (21: 1.0: 0.6); *Pentidotea resecata* (15: 0.2: 0.6); *Excorallana kathae* (3: 0.1: 1.0); *Cirolana diminuta* (15: 0.2: 0.2); *Rocinella belliceps* (6: <0.1: 0.2); *Exospheroma* sp. (6: <0.1: <0.1); idoteid sp. (3: <0.1: 0.1).
4. CAPRELLID AMPHIPODS (41: 2.1: 6.0)
   Caprella pilidigita (24: 1.4: 4.7); *C. californica* (21: 0.7: 1.2); *C. penantis* (3: <0.1: <0.1); *Tritella laevis* (3: <0.1: <0.1).
5. POLYCHAETES, SWIMMING (35: <0.7: 6.4)
   epitokous nereids (9: 0.7: 5.5); unidentified fragments (26: ?: 0.9).
6. OSTRACODS (62: 1.7: 1.6)
   Parasterope sp. A (38: 0.7: 0.6); *Cycloleberis lobiancoi* (23: 0.5: 0.4); *Philomedes* sp. (9: 0.4: 0.4); species O (3: <0.1: <0.1); species N (3: <0.1: <0.1).
7. MYSIDS (21: 0.6: 1.3)
   Siriella pacifica (15: 0.5: 1.2); *Acanthomysis sculpta* (3: <0.1: <0.1); unidentified fragments (3: 0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (21: 0.9: 0.9)
   Hippolyte clarki (3: 0.2: 0.1); unidentified (24: 0.7: 0.8).
9. BRACHYURAN MEGALOPS (26: 0.7: 0.5)
   unidentified.
10. TANAIDS (15: 0.5: 0.5)
    Leptochelia dubia (6: 0.2: 0.3); unidentified (9: 0.3: 0.2).
11. NEBALIACEANS (6: <0.1: <0.1)
    Nebalia pugettensis.
12. CARIDEAN LARVAE (3: <0.1: <0.1)
    unidentified.

Brachyistius frenatus—kelp perch

The kelp perch, which Miller and Lea (1972) claimed can attain a length of 214 mm, was numerous close among the rising stands of giant kelp. It often aggregated immediately under the canopy (Figure 11), but occurred along the entire length of the plants from water's surface to the

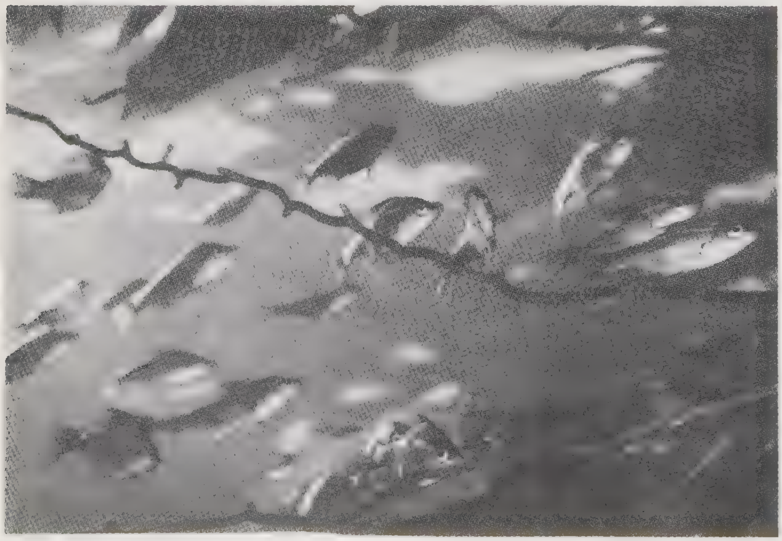


FIGURE 11.—Kelp perch, *Brachyistius frenatus*, aggregated close to kelp, pluck zooplankters from the water column during the day.

sea floor, with larger individuals mostly in the lower regions. Far fewer numbers also occurred close above low fields of benthic algae some distance from the kelp forest. It assumed similar attitudes in the same places during both day and night, but after dark there seemed to be more of them in the mid-waters along the outer edge of the kelp.

Most kelp perch feed by plucking material from the surface of algae, but plankton-feeding is widespread, especially among those aggregated in the mid-waters at the edges of the forests. Limbaugh (1955) reported that the kelp perch feeds on small crustaceans, particularly those that occur on giant kelp. Quast (1968) also reported a predominantly crustacean diet, with a preponderance of amphipods, but also including mollusks and bryozoans.

Preliminary assessment of our food-habit data, along with direct observations, showed that in this species it is primarily the smaller individuals that feed on plankton. Consequently, we consider for this paper only those less than 100 mm long, leaving the larger individuals for a later paper. This point is drawn somewhat arbitrarily, although plankters generally become noticeably less prevalent in the diet at about this size. With kelp perch more so than with the other species treated in this paper, however, many of the individuals considered had mixed a diet of plankters with organisms plucked from a substrate. Bray and Ebeling (1975) reported that kelp perch feed mainly on tiny plankters, mostly copepods, based on a sample of predominantly small individuals (43-142 mm, $\bar{x}$ = 103).

All 35 specimens (40-99 mm $\bar{x}$ = 81) collected during the afternoon as they swam over various locations in the study area, usually close to kelp, contained food, much of it fresh. On the other hand, of 34 specimens (38-99 mm, $\bar{x}$ = 76) collected during the 2 h of night before first morning light 25 (74%) were empty. The other nine, however, contained food, including relatively fresh items. Thus, although the kelp perch within this size range clearly fed mostly by day, some apparently fed at night. Individuals evidencing nocturnal feeding ranged from 81 to 99 ($\bar{x}$ = 95) mm long, and so were among the larger ones in the sample.

Recognizing that the contrasting conditions between day and night undoubtedly influenced the composition of the diet, food data from individuals collected during the afternoon (when presumably most fresh items in the gut had been taken by day) were considered separately from food data from individuals collected during the last hours of the night (when presumably most fresh items in the gut had been taken after dark).

In addition to the high incidence of empty guts in kelp perch collected at night, the guts of those that had taken prey after dark averaged 50% full, compared with an average of 72% full for the day feeders. Furthermore, the night feeders contained an average of 38 prey items, compared with an average of 252 for the day feeders (at least in part, however, this difference reflects the larger size of nocturnal prey). These data strengthen our conclusion that over the size range studied, nocturnal feeding is relatively unimportant to this species. Bray and Ebeling (1975) also noted that kelp perch feed mainly by day.

Foods taken by individuals that had been feeding during the day are ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (94: 157.7: 49.1)
   calanoids, including *Calanus pacificas*, and *Rhincalanus nasutus* (71: 137.2: 44.2); cyclopoids, including *Corycaeus* sp. and *Oncea* sp. (74: 20.5: 4.9).
2. GAMMARIDEAN AMPHIPODS (63: 57.9: 37.0)
   Microjassa litodes (46: 23.1: 15.1); *Ericthonias braziliensis* (14: 3.9: 2.6); *Gitanopsis vilordes* (11: 3.0: 0.1); *Ampithoe* spp. (3: 0.1: 0.2); *Hyale nigra* (3: 0.3: 0.2); *Batea transversa* (3: 0.1: 0.1); unidentified (63: 27.4: 18.7).
3. CLADOCERANS (37: 26.1: 6.9)
   Evadne sp.
4. CIRRIPEDIAN LARVAE (31: 1.8: 0.9)
   cypris stage.
5. POLYCHAETES, NONSWIMMING (11: 0.4: 1.9)
   Spirorbis sp. (9: 0.4: 1.8); unidentified (3: 0.1: 0.1).
6. HARPACTICOID COPEPODS (14: 1.6: 0.7)
   Porcellidium sp. A (11: 1.5: 0.6); *Porcellidium* sp. B (3: 0.1: 0.1).
7. OSTRACODS (26: 0.6: 0.6)
   Cythereis sp. (17: 0.3: 0.2); *Philomedes* sp. B (11: 0.2: 0.1); unidentified sp. C (3: 0.1: 0.3).
8. CAPRELLID AMPHIPODS (9: 0.3: 0.7)
   Caprella pilidigita (6: 0.2: 0.4); *C. californica* (3: <0.1: 0.3).
9. FISH EGGS (14: 0.4: 0.3)
   unidentified.
10. PELECYPODS (11: 0.4: 0.3)
    Hiatella arctica (9: 0.3: 0.3); *Halodakra brunnea* (3: <0.1: <0.1).
11. ISOPODS (14: 0.7: 0.2)
    Paracercies sp. (6: 0.5: 0.1); gnathiid juveniles (6: 0.1: <0.1); unidentified fragments (3: 0.1: 0.1).
12. BRYOZOAN LARVAE (9: 0.1: 0.2)
    cyphonautes.
13. CARIDEAN LARVAE (9: 0.2: <0.1)
    unidentified.
14. FISHES (6: 0.2: <0.1)
    unidentified larvae.

15. MYSIDS (3: <0.1: <0.1)
    Siriella pacifica.
16. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.
17. CARIDEAN ADULTS AND JUVENILES (3: <0.1: <0.1)
    Hippolyte clarki.

Although these fish preyed heavily on zooplankters, clearly many of the organisms in the above list were plucked from a substrate. The major gammaridean, *Microjassa litodes*, was never seen or taken by us in the water column, but was a predominent form on the surface of giant kelp (Hobson and Chess in prep.) Similarly, the many forms known to occur in the water column only at night, e.g., *Siriella pacifica*, *Cyclaspis nubila*, *Paracercies* sp., *Batea transversa*, and *Hippolyte clarki* were probably plucked by these day feeders from the algae or sand where they occur in the daytime.

Foods taken by individuals that had been feeding at night are ranked below.

1. GAMMARIDEAN AMPHIPODS (100: 33.8: 71.1)
   Batea transversa (66: 8.1: 22.1); *Ericthonias braziliensis* (44: 0.9: 2.6); *Microjassa litodes* (22: 1.6: 1.7); *Ampithoe* spp. (22: 0.3: 0.9); *Hyale nigra* (11: 0.4: 0.9); *Aoroides columbiae* (11: 0.1: 0.3); unidentified, at least some probably juveniles of the above (100: 22.4: 42.6).
2. CAPRELLID AMPHIPODS (66: 4.4: 15.0)
   Caprella californica (55: 2.0: 9.5); *C. pilidigita* (11: 2.0: 4.1); unidentified (22: 0.4: 1.4).
3. ISOPODS (44: 0.5: 6.6)
   Paracercies sp.
4. CARIDEAN ADULTS AND JUVENILES (55: 0.7: 5.1)
   unidentified.
5. MYSIDS (22: 0.2: 1.1)
   Siriella pacifica (12: 0.1: 1.0); erythropinid sp. (11: 0.1: 0.1).
6. POLYCHAETES, NONSWIMMING (22: 0.2: 0.3)
   Spirorbis sp.
7. OSTRACODS (22: 0.2: 0.2)
   Parasterope sp. A (12: 0.1: 0.1); *Cytheresis* sp. (11: 0.1: 0.1).
8. FORAMINIFERANS (11: 0.1: 0.2)
   unidentified.
9. HARPACTICOID COPEPODS (11: 1.0: 0.1)
   Porcellidium sp. A.

Two specimens also contained fragments of algae (*Macrocystis* in one, *Sargassum* in the other) that probably had been taken incidentally along with prey. Clearly this fish took at least some of its nocturnal prey from a substrate—*Spirorbis* sp., for example. Nevertheless, because the diet is comprised mostly of organisms that swim in the water column at night, we believe this was probably where most of them were taken. Most of these prey organisms also occurred on rocks and algae after dark, but if substrate-feeding had predominated, we would have expected a greater proportion of strictly substrate-dwelling forms.

Oxyjulis californica—señorita

The señorita, which can attain a length of 250 mm (Miller and Lea 1972), is perhaps the most widespread fish in nearshore habitats at Santa Catalina Island. It is strictly a diurnal species that, like other labrids, rests under cover on the sea floor at night (Hobson 1971). Often during the day it swims in large assemblages 1 to 2 m above the sea floor (Figure 12).

Most señoritas feed by plucking material from the surface of algae—often from algae drifting as fragments in the mid-waters—but plankton-feeding is widespread, and predominates in smaller juveniles. Limbaugh (1955) concluded that the señorita is an omnivorous carnivore that feeds "on almost any animal protein." Hobson (1971) found that specimens between 110 and 195 mm long had fed primarily on bryozoans that encrust algae, and on caprellid amphipods. Quast (1968) reported the principal foods to be small gastropods and crustaceans commonly associated with algae, but noted that specimens 50 to 60 mm long had fed heavily on copepods, ostracods, and bryozoan larvae.

Direct observations, complemented by our food habit data (see below), agree that smaller individuals mostly pluck their prey from the water column, whereas larger individuals mostly pluck their prey from some substrate. In this respect, then, the señorita is similar to the kelp perch, described above. So, as with the kelp perch, this paper considers only those individuals less than 100 mm long, leaving the larger individuals for a later paper. We have better reason for drawing the dichotomy at this point with the señorita than with the kelp perch: the smallest señorita we found containing prey obviously plucked from a substrate was 101 mm long, and although planktivorous habits predominated in certain individuals up to 175 mm (which were among the largest taken), most over 100 mm seemed to feed primarily on a substrate. So unlike the diverse feeding habits of smaller kelp perch, the smaller señoritas seemed strictly planktivorous. Bray and Ebeling (1975) stated: "Unlike kelp perch, señoritas did not exploit the plankton as a major source of food." Although this view would seem to disagree with our findings, their samples of the two species were not comparable on this point. Most of their kelp

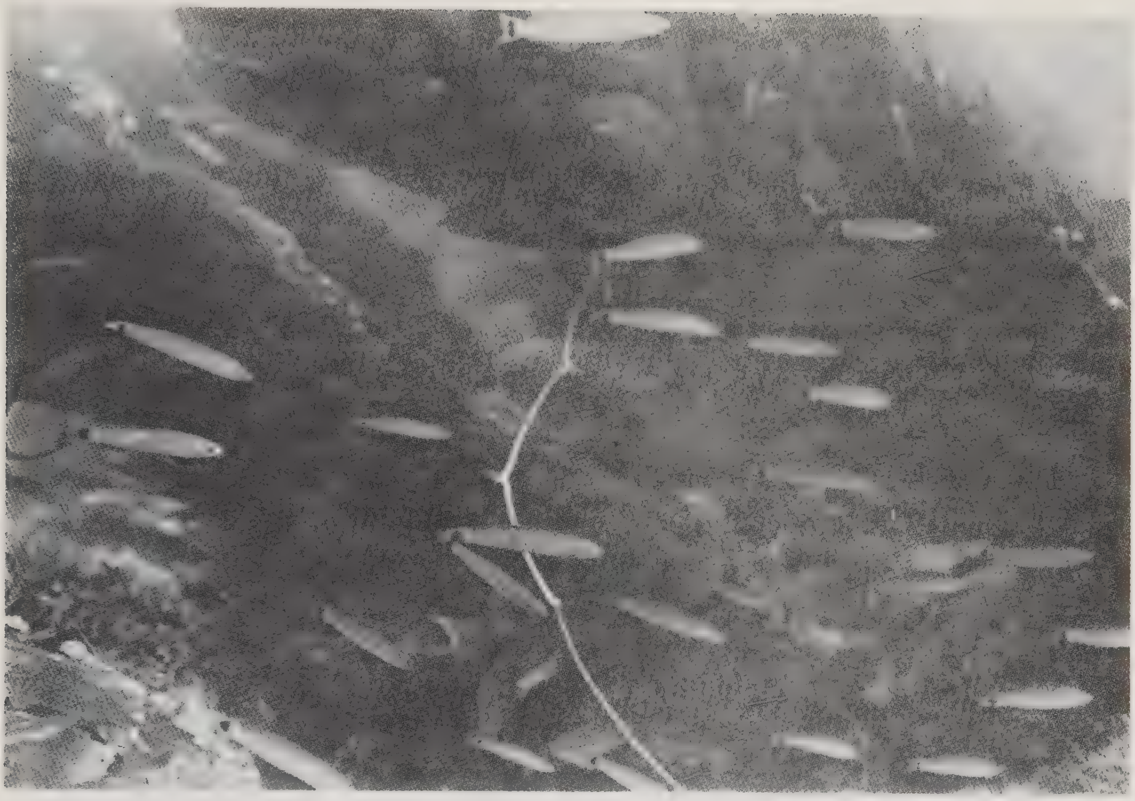


FIGURE 12.–An aggregation of señoritas, *Oxyjulis californica*, passes along the edge of a kelp forest during the day.

perch were small, as noted above, whereas their señoritas were relatively large (110-223 mm, $\bar{x}$ = 169).

All 24 specimens (19-99 mm, $\bar{x}$ = 51) collected during the afternoon as they swam in groups above the sea floor were full of relatively fresh prey, as ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (100: 68.7: 74.1) calanoids (75: 44.3: 43.8); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (67: 24.4: 30.3).
2. BRYOZOAN LARVAE (58: 7.3: 4.3) cyphonautes.
3. HARPACTICOID COPEPODS (42: 7.1: 4.8) *Microsetella* sp. (25: 3.1: 2.1); *Porcellidium* sp. A (8: 0.1: 0.2); unidentified spp. (21: 3.9: 2.5).
4. CIRRIPEDIAN LARVAE (46: 2.8: 2.8) cypris stage.
5. GAMMARIDEAN AMPHIPODS (25: 1.8: 4.7) unidentified fragments.
6. CLADOCERANS (21: 4.8: 5.4) *Evadne* sp.
7. MOLLUSK LARVAE (46: 1.1: 1.0) veligers.
8. FISH EGGS (4: 0.1: 0.3) unidentified.
9. RADIOLARIANS (4: 0.1: <0.1) unidentified.

With the likely exception of the gammarideans, which were unidentifiable, all of the items in the above list are organisms present in the water column at the time these fish were feeding.

Chromis punctipinnis—blacksmith

The blacksmith, which can attain a length of 300 mm (Miller and Lea 1972), is probably the most numerous fish in the nearshore waters at Santa Catalina Island. During the day it concentrated along the seaward edge of the kelp forests, but occurred in varying numbers in most nearshore habitats, usually aggregated in the mid-waters (Figure 13). At nightfall it sheltered among the rocks, often considerable distances inshore from where it spent the day.

Other species of the genus *Chromis* are widespread in tropical seas, where they are known to be planktivores, e.g.: West Indies (Randall 1967); Gulf

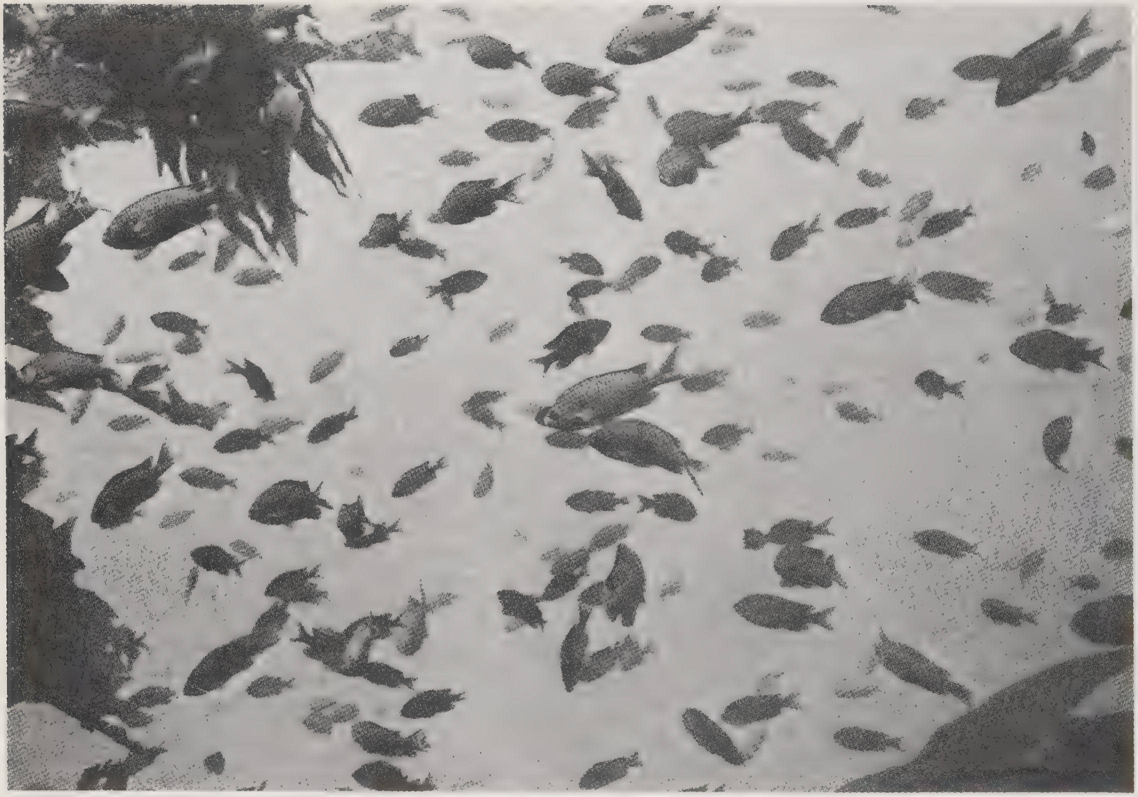


FIGURE 13.–Blacksmiths, *Chromis punctipinnis*, aggregated at the edge of a kelp forest, pluck zooplankters from the water column during the day.

of California (Hobson 1968); Hawaii (Swerdloff 1970; Hobson 1974). It is also well-known that *C. punctipinnis* is a planktivore. Limbaugh (1955) noted that it feeds on "particulate plankton such as small fish, squid, and crustaceans," and "may materially affect the amount of plankton entering kelp beds because they eat it as it enters." Quast (1968) listed the principal food of the blacksmith as "minute swimming crustacea and crustacean eggs and larvae gleaned from open water species of kelp beds and over rocky areas." In taking its tiny prey from the water column in what seems a visually directed action, the blacksmith suddenly thrusts both of its highly protrusible jaws forward, then immediately retracts them, presumably sucking plankters into its rapidly expanding oral cavity. This way of feeding has also been noted among its tropical congeners (Swerdloff 1970; Hobson 1974).

Aggregations of blacksmiths feeding on plankton occurred throughout the water column, with each member of an aggregation acting independently. They aggregated according to size: the discrete aggregations of small juveniles (which first appeared inshore during late summer, when about 15 to 25 mm long) generally were closer to the sea floor than were aggregations of the adults.

Blacksmiths fed throughout the day, but the rate at which they ingested prey varied. In the tropical Atlantic, *Eupomacentrus partitus*, another planktivorous pomacentrid, feeds more rapidly with increased light and with increased current (Stevenson 1972). Blacksmiths, too, feed more rapidly in a current than at slack water, presumably (as Stevenson suggested of *E. partitus*) because they receive more plankters. To measure this effect, we counted the characteristic mouth movements of feeding adult blacksmiths, first in a moderate current, and then at slack water. The observations were made during midafternoon under a clear sky at a depth of 5 m in 10 m of water. The fish were part of an aggregation with members ranging from about 109 to 130 mm long (these being the sizes of the two individuals collected later judged to be the largest and smallest in the group). In the moderate current, with the giant kelp lying over at about 25° (attempts to measure the current in this habitat proved unsatisfactory owing to complex eddy systems), 10 individuals (selected haphazardly) plucked at plankters 50 to 73 ($\bar{x} = 58$) times during 1-min periods. One hour later, when there was no discernible current, 10 individuals in a similar, if not the same aggregation, each plucked at plankters 30 to 51 ($\bar{x} = 39$) times during 1-min periods. Probably there is an optimum current speed beyond which the fish find the increasing difficulty of maintaining station outweighs the advantage of added food. We lack data on feeding rates, but have noted that in strong currents blacksmiths abandon the open places within the forest, where they had been dispersed and feeding, and concentrate in dense numbers close in the lee of individual kelp columns.

Of 41 adults (92-145 mm, $\bar{x} = 118$) collected from aggregations in the water column throughout the study area during the afternoons, 36 were full of food, much of it fresh. The other 5, all collected during midafternoon along the margin of the forest bordering the inshore edge of the *Dictyopteris* field, were empty. All prey taken by these blacksmiths, ranked below, are forms we have collected in the water column during the day.

1. LARVACEANS (100: 448.1: 57.5)
   most of them *Oikopleura* spp.
2. CALANOID AND CYCLOPOID COPEPODS (100: 256.3: 33.7)
   calanoids, including *Calanus pacificus*, *Acartia tonsa*, *Labidocera* sp., and *Rhincalanus nasutus* (100: 253.6: 32.4); cyclopoids, including *Corycaeus* sp., *Oncaea* sp., and *Oithona* sp. (72: 2.7: 1.3).
3. FISH EGGS (69: 17.9: 4.1)
   unidentified.
4. CLADOCERANS (75: 24.6: 2.5)
   Evadne spp.
5. CARIDEAN LARVAE (33: 1.4: 0.9)
   unidentified.
6. EUPHAUSID LARVAE (33: 5.1: 0.6)
   calyptopis stage.
7. CIRRIPEDIAN LARVAE (33: 3.5: 0.6)
   cypris stage.
8. BRYOZOAN LARVAE (17: 1.2: 0.2)
   cyphonautes.
9. CHAETOGNATHS (3: 0.1: 0.5)
   unidentified.
10. REPTANTIAN ZOEA (3: 0.4: 0.1)
    unidentified.
11. HARPACTICOID COPEPODS (3: <0.1: <0.1)
    Microsetella sp. A.
12. FISHES (3: <0.1: <0.1)
    unidentified larvae.
13. ISOPODS (3: <0.1: <0.1)
    gnathiid juvenile.

In feeding so heavily on larvaceans, their major prey, these adult blacksmiths differ from other species treated in this report. Significantly, however, larvaceans are also major prey of other species of *Chromis* elsewhere, e.g., in Hawaii (Hobson 1974) and in the West Indies (Randall 1967). Probably larvaceans are important food of the blacksmith throughout its range, even though they have gone unreported in previous food-habit studies of this species. Larvaceans are difficult to recognize, especially if digestion is advanced or preservation faulty, and this may account for them going unreported.

Because juvenile blacksmiths were in feeding aggregations distinct from those of the adults, we analyzed their gut contents separately. Of 14 juveniles (16-47 mm, $\bar{x} = 34$) collected from aggregations during the afternoon, all were full of food, much of it fresh. All prey, ranked below, are forms that we have collected from the water column during the day.

1. CALANOID AND CYCLOPOID COPEPODS (100: 394.4: 54.1)
   calanoids, including *Acartia tonsa* (100: 366.2: 50.5); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (93: 28.2: 3.6).
2. LARVACEANS (93: 48.9: 26.4)
   most of them *Oikopleura* spp.
3. CLADOCERANS (100: 108.8: 12.5)
   Evadne spp.
4. CIRRIPEDIAN LARVAE (79: 63.6: 4.6)
   cypris stage.
5. BRYOZOAN LARVAE (79: 63.6: 4.6)
   cyphonautes.
6. HARPACTICOID COPEPODS (57: 6.4: 0.8)
   Microsetella sp. A.
7. FISH EGGS (43: 2.1: 0.7)
   unidentified.

Differences in the diet between juvenile and adult blacksmiths can be related to the sizes of the various organisms in the water column. Most prey of the juveniles were less than 0.5 mm long. Compared to the prey of adults these included more cladocerans, copepods, and larvae of barnacles and bryozoans, but fewer larvaceans and fish eggs (there were no larvaceans in the smallest blacksmith, 16 mm long, and no fish eggs in all six <34 mm).

During the day, the heaviest concentrations of adult blacksmiths in the vicinity of the study area were at the mouth of the cove seaward of the kelp forest. The sea floor in this region is sand, and lies under more than 30 m of water. Because blacksmiths habitually settled among rocks at night, the offshore feeders migrated to resting areas inshore at day's end. At the migration's peak, groups of 100 or more blacksmiths spaced perhaps 50 m apart streamed along established routes.

As the migrators swam between feeding grounds and shelter areas, they passed among many other blacksmiths, most of which were actively feeding and which gave the migrators no overt notice. Most of the blacksmiths in the vicinity of the study area were nonmigrators that found nocturnal shelter among rocks lying below their mid-water feeding grounds.

Most of the blacksmiths within the forest bordering the study area began descending toward the sea floor by sunset, and by 35 min after sunset the vast majority had taken shelter among the rocks. They rested here throughout the night, and their lack of feeding during this period is indicated by the empty guts we found in all 11 individuals (111-143 mm, $\bar{x}$ = 122) collected among rocks during the 2 h immediately before first morning light.

In the morning, blacksmiths among the rocks became noticeably active about 40 min before sunrise. They began to rise among the kelp columns about 25 to 30 min before sunrise, and to feed about 5 to 10 min later. At about the same time that blacksmiths within the forest were rising into the water column, the migrating individuals streamed along their courses to the offshore feeding grounds, reversing the courses they had followed inshore the night before.

DISCUSSION

Trophic relationships among the fishes and zooplankters near shore at Santa Catalina Island differ strikingly between day and night (Table 9), broadly paralleling the situation described earlier in the water column above tropical reefs (Hobson 1965, 1968, 1972, 1973, 1974). This section discusses these differences and their evolutionary implications.

The Mid-Waters in Daylight

Zooplankters populating the nearshore water column at Santa Catalina during the day—including radiolarians, cladocerans, copepods, and

TABLE 9.—Percent of each fish species that took prey in each major food category.

	Day feeders 1. olive rockfish <55 mm, *n* = 42 2. kelp perch <100 mm, *n* = 35 3. señorita <100 mm, *n* = 24 4. blacksmith >90 mm, *n* = 36 5. blacksmith <50 mm, *n* = 14					Night feeders 1. olive rockfish >65 mm, *n* = 70 2. kelp rockfish, *n* = 20 3. salema, *n* = 5 4. queenfish, *n* = 32 5. walleye surfperch, *n* = 34 6. kelp perch <100 mm, *n* = 9					
Major food category	1	2	3	4	5	1	2	3	4	5	6
Radiolarians	0	0	4	0	0	0	0	0	0	0	0
Polychaetes, swimming	0	0	0	0	0	36	20	40	31	35	0
Mollusk larvae	0	0	46	0	0	0	0	0	0	0	0
Cladocerans	20	37	21	75	100	0	0	0	0	0	0
Ostracods	0	26	0	0	0	43	30	80	13	62	22
Calanoid and cyclopoid copepods	83	94	100	100	100	4	0	20	0	0	0
Harpacticoid copepods	18	14	42	3	57	13	0	0	0	0	11
Other copepods	18	0	0	0	0	1	0	0	0	0	0
Cirripedian larvae	5	31	46	33	79	0	0	0	0	0	0
Nebeliaceans	0	0	0	0	0	1	5	20	6	6	0
Mysids	11	3	0	0	0	69	90	100	84	21	22
Cumaceans	0	3	0	0	0	57	5	60	3	85	0
Tanaids	10	0	0	0	0	26	0	0	0	15	0
Isopods	2	14	0	3	0	39	75	40	34	72	44
Gammaridean amphipods	29	63	25	0	0	90	95	100	89	100	100
Caprellid amphipods	0	9	0	0	0	36	0	40	0	41	66
Euphausid larvae	2	0	0	33	0	0	0	0	0	0	0
Euphausid adults and juveniles	11	0	0	0	0	7	5	0	3	0	0
Caridean larvae	20	9	0	33	0	9	0	20	3	3	0
Caridean adults and juveniles	0	3	0	0	0	24	85	20	44	21	55
Reptantian zoea	11	0	0	3	0	6	0	20	0	0	0
Brachyuran megalops	5	0	0	0	0	10	0	0	3	26	0
Bryozoan larvae	2	9	58	17	79	0	0	0	0	0	0
Chaetognaths	0	0	0	3	0	0	0	0	0	0	0
Larvaceans	0	0	0	100	93	0	0	0	0	0	0
Fish eggs	0	14	4	69	43	0	0	0	0	0	0
Fishes	5	6	0	3	0	9	15	20	6	0	0
Other	2	22	0	0	0	0	15	0	0	0	33

various larval forms (see Tables 1, 2)—tend to be less than 2 mm in their greatest dimension. Forms appreciably larger than this—including chaetognaths and some larvaceans—tend to be transparent. These organisms are equally numerous in the water column at night, and none are residents of the study area. The species are widespread in the water columns of the various inshore habitats, and also offshore.

This assemblage resists a common label. Most of the species have been considered holoplankton (planktonic throughout the whole of their life histories: Newell and Newell 1963), but this term excludes the larval forms so prominent here. The larval forms generally are considered meroplankton (planktonic during some stage in their life histories, but benthonic during some other: Newell and Newell 1963), but this term has been used in general reference to organisms that are planktonic at night, but benthonic by day (e.g., Williams and Bynum 1972). As noted above, we do not use these terms because they fail to define categories meaningful to the concepts developed in this paper.

Fishes that forage in the water column by day have certain characteristics relating to the problems they face as diurnal planktivores. Significantly, of the four diurnal planktivores studied at Santa Catalina, three—the señorita, the kelp perch, and the small juvenile olive rockfish—outgrow this habit. Apparently as they grow larger they find the tiny organisms in the mid-waters increasingly inappropriate as prey. We believe that each is limited in taking very small prey by the size and structure of its mouth, a problem solved by changing either feeding place, or feeding time. Thus, the señorita and kelp perch (noted by Hubbs and Hubbs 1954, to have similar dentition and feeding habits) increasingly abandon the water column as a hunting ground as they grow and shift to prey on organisms that live on algae. The small juvenile olive rockfish, on the other hand, continues to feed in the water column, but assumes nocturnal habits that bring it into contact with the larger organisms that rise above the sea floor at night (see below). The señorita and kelp perch, both relatively small-mouthed species, generally shift their food habits when about 100 mm long; the olive rockfish, with a much larger mouth (compare Figures 6, 11, 12), generally shifts when under 65 mm long.

The fourth diurnal planktivore studied at Santa Catalina, the blacksmith, retains its planktivorous diet through adulthood. It does so despite growing to a relatively large size because it has, among other adaptive features, a small mouth specialized for this habit. Judging from its numbers, the blacksmith is highly successful in the warm temperate waters of southern California. But it does not range far into the colder waters northward, and all its many congeners live in the tropics. The blacksmith embodies morphological features uncharacteristic of temperate-zone fishes, but which are widespread among tropical species. In writing of reef fishes in the tropical Atlantic Ocean, Davis and Birdsong (1973) described morphological specializations adaptive for foraging on small organisms in the mid-waters, and although they do not make the point, all their examples are species that feed by day. Especially striking are the modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively capture tiny prey in open water.

The Mid-Waters at Night

The nocturnal zooplankton include, in addition to the organisms also present during the day, a large array of forms that rise at the onset of darkness from daytime shelters on, in, or close to the sea floor or other cover. These nocturnal additions to the zooplankton include various polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, isopods, tanaids, carideans, and others (see Tables 1, 2). Most exceed 2 mm in their greatest dimension, and many are 7 to 10 mm, and longer. Unlike the full-time zooplankters, which have no particular relation to the study area, these part-time zooplankters are local residents that rise at night from substrata they are closely associated with during the day.

The nocturnal components of the zooplankton seem to have reasons for rising into the water column at night that are as diverse as their morphologies. Because they have diverse habits that are little known, we feel that terms defining ecological categories among them are premature. Bousfield (1973), and others, have referred to many such forms as tychoplankton, but this term implies that presence in the water column is by chance, or accident—a description that fits very few, if any, of the forms considered here. Many are nocturnal feeders; e.g., when the mysid *Siriella pacifica* moves into the mid-waters after dark, it feeds on copepods and other smaller zooplankters. Similarly, nocturnal foraging may be the rule among species like the ostracod *Perasterope* sp. A, the cumacean *Cumella* sp. A, and the amphipod *Batea transversa*, where it seems the majority spend most of the night in the water column. Working in the tropical Atlantic Ocean, Emery (1968) noted that polychaetes, cumaceans, and zoea rise into the water column at night after spending the day under reef shelter and speculated that they make this ascent to forage. But most of the polychaetes entering the water column after dark at Santa Catalina are epitokus nereids, whose mid-water activities probably relate to reproduction.

Williams and Bynum (1972) doubted the nightly ascents of amphipods in North Carolina estuaries relate to feeding because they subsist on detritus. But detritus can be available to zooplankters in the water column, as reported by Gerber and Marshall (1974) from a coral atoll in the central Pacific. Significantly, however, many of the amphipods that enter the mid-waters at night appear morphologically maladapted for swimming. The oedicerotids (including *Monoculodes* and *Synchelidium*), for example, are modified for burrowing in unstable sand (Bousfield 1973), and the caprellids (Figure 5V) seem especially unsuited for existence in mid-water. It is unlikely that such forms are in the water column to feed, especially as relatively small proportions of their populations are up there. Probably these and similar forms make only brief, or infrequent excursions into the water column for reasons yet undetermined. Williams and Bynum (1972) suggested that relative numbers of caprellids entering the water column may correlate with seasonal deterioration of their benthic habitats. They also felt that among gammaridean amphipods the tubicolous forms (e.g., *Ampelisca* and *Ericthonias*) may facilitate reproduction by entering the water column, where mating pairs would have free access to each other.

We reject Williams and Bynum's additional suggestion that the nightly ascent may be an attempt to escape from predatory bottom-feeding fishes. Most bottom-feeding fishes that prey heavily on amphipods (and other similar organisms) are diurnal. (Some of the relatively few fishes that prey on amphipods at night, and the circumstances surrounding this predation, will be discussed later; Hobson and Chess in prep.) Most predaceous fishes feed visually, and tiny, cryptically hued forms on dark substrata seem to go unseen in the low levels of illumination that prevail at night (Hobson and Chess in prep.; see also Hobson 1968, 1974, for accounts of the same situation on tropical reefs). For whatever the reason, most amphipods that fall prey to predatory fishes after dark are species that rise into the water column.

Compared to their diurnal counterparts, the nocturnal planktivorous fishes are of relatively large sizes and have large mouths—both characteristics reflecting the relatively large size and accessibility of organisms in the mid-waters after dark.

Evolutionary Implications

Since early in the Mesozoic period, the evolution of actinopterigian fishes has centered on a mainstream of generalized predators (Schaeffer and Rosen 1961). Because such predators are adapted for straightforward attacks at prey in exposed positions, the water column, with its absence of cover, has been a risky place for smaller organisms throughout the evolution of modern nearshore marine communities. In discussing the earliest actinopterigian fishes, Schaeffer and Rosen stated that food was probably first obtained by biting and was swallowed whole. Although advances in mouth structure have refined their means of seizing food (Schaeffer and Rosen 1961; Gosline 1971), generalized teleosts have continued to take their prey intact. Consequently, these fishes have found appropriate prey to be organisms large enough for them to entrap in their relatively large mouths, yet small enough for them to swallow whole. As demonstrated at Santa Catalina, prey of appropriate size include animals that rise into the nearshore water column after dark—mysids, amphipods, isopods, and others.

The present situation at Santa Catalina Island suggests that since early times predation pressures from large-mouthed, generalized predators have influenced major evolutionary trends among shallow-water zooplankters. Most apparent are trends toward nocturnal planktonic activity in those zooplankters that would spend only part of their time in the water column, and toward reduced size among those zooplankters that would spend all of their time in the water column. At the same time it would appear that each of these trends has elicited an evolutionary response among planktivorous fishes, as discussed below. We do not suggested that pressures exerted in predator-prey interactions have been the only force shaping these trends, but we believe their impact has been significant. (A trend toward transparency, most developed in the larger zooplankters present in the water column during the day, is obviously adaptive for organisms threatened by visually feeding predators. Although this trend is only briefly mentioned here, its importance in defense against predators is emphasized by Hamner et al. 1975.)

Because most generalized predaceous fishes probably have been visual feeders since early times, their prey would have long since found water-column activities most safely performed under cover of darkness. Not surprisingly, the zooplankters that are vulnerable to large-mouthed fishes are mostly nocturnal forms that spend the daytime amid benthic cover. But only organisms that have the capacity to leave the water column can enjoy the advantage of cover during vulnerable periods.

The organisms that spend all their time in the water column have had to adapt to being fully exposed during daylight, when the visual sense of their predators is most effective. Under this circumstance one would expect long-established selective pressures favoring sizes smaller than those that can be entrapped by the relatively large mouths of generalized predators. That such selective pressures operate today among zooplankters in daylight is well documented. Brooks and Dotson (1965), for example, described the larger zooplankters in a lake being eliminated by the planktivorous clupeoid fish *Alosa pseudoharengus*, reported by Emery (1973) to feed by day.

Because successful defenses in prey create pressures that modify the offenses of predators, early tendencies in prey toward nocturnal habits or reduced size would have generated appropriate evolutionary responses among predators. Certainly a long-standing selection for nocturnal capabilities is evidenced by the many large-mouthed predaceous fishes that forage in the mid-waters at Santa Catalina after dark, including the walleye, the salema, and the queenfish. Large eyes, an obvious advantage in predators that hunt at night, have been widely acquired by these fishes (see Figures 6-10). Similarly, the small mouth and other specialized features of diurnal planktivorous fishes, like the blacksmith, clearly are adaptive for feeding on the very small organisms that constitute the diurnal zooplankton (see Figures 11-13). In their feeding morphologies and body forms, the nocturnal planktivores have diverged less than have their diurnal counterparts from the generalized predators that gave rise to them all. This does not necessarily mean that the diurnal planktivores are more recently evolved. Each is the product of an equally long evolution, and while the diurnal planktivores have been molded by selective pressures favoring the capacity to take tiny organisms, the nocturnal species have been influenced during the same period by selective pressures favoring the capacity to detect and capture prey in the dark.

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CULTURE AND GROWTH OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE

JOHN R. HUNTER[1]

ABSTRACT

Culture techniques used to rear larval anchovy through metamorphosis using laboratory cultured foods are described. Anchovy larvae fed dinoflagellates *Gymnodinium splendens*, rotifers *Brachionus plicatilis*, harpacticoid copepods *Tisbe furcata*, and brine shrimp nauplii *Artemia salina*, completed metamorphosis (35 mm) in 74 days at 16°C with a minimum survival of 12.5%. Growth in length and weight were recorded over this interval and an excellent fit to the Laird-Gompertz growth equation was obtained. Growth was comparable to that on a wild plankton diet. In a starvation experiment, most of the fish that completed metamorphosis withstood a starvation period of 12-15 days, whereas those that had not completed metamorphosis did not.

Knowledge of the growth rate of northern anchovy, *Engraulis mordax* Girard, is essential for estimating year class success or larval survival. Another important element in estimating survival is the time fish or larvae can withstand starvation. In this report I describe the growth rate of larval anchovy to metamorphosis and present data on the ability of newly metamorphosed juveniles to withstand starvation. Special attention is also given to culture techniques because this is the first time northern anchovy have been reared through metamorphosis entirely on cultured foods.

Kramer and Zweifel (1970) recorded the growth of anchovy larvae at 17° and 22°C for periods of up to 34 days. In their experiments larvae attained an average length of 17 mm but did not reach metamorphosis, which is complete at about 35 mm standard length. Their larvae were fed wild plankton supplemented by *Artemia salina* nauplii. In the ensuing years, rearing techniques using cultured foods have gradually been developed: *Gymnodinium splendens* for 3- to 5-day-old larvae (Lasker et al. 1970), and *Brachionus plicatilis* for 5- to 20-day-old larvae (Theilacker and McMaster 1971). This paper describes the use of the harpacticoid copepod *Tisbe furcata* which are the proper size food for larvae older than 20 days (10 mm). All previous attempts to rear anchovy larvae beyond 35 days on cultured foods have failed. In all attempts *Artemia* nauplii were used after 20 days.

METHODS

Five rearing experiments were done, four at 16°C and one at 17° to 18°C (Table 1). Eggs for all experiments were obtained from a captive population of anchovy which were maintained in breeding condition continuously at the Southwest Fisheries Center La Jolla Laboratory (Leong 1971).

Rearing tanks were cylindrical, black fiberglass, 122 cm diameter, 36 cm deep, covered with a transparent acrylic plastic top, and immersed in a water bath regulated by a refrigeration unit. Temperature was maintained near 16°C in all but one experiment, and the salinity was 35‰. Fluorescent lamps suspended directly over each tank provided about 2,000 lx at the water surface. The volume of water in the tanks gradually increased from an initial volume of 200 liters of filtered seawater to 400 liters by about 20 days because of additions of seawater containing algae and food organisms. Thereafter, the volume was maintained at about 400 liters by siphoning water from the bottom from time to time which also cleaned the tank.

Records were kept of the quantity of food or algae added to tanks and on alternate days 16, 0.20-ml aliquots were taken to measure the density of *Brachionus plicatilis*, *Gymnodinium splendens*, and *Artemia salina* nauplii in the tanks. Concentrations of *Tisbe furcata* in the tanks were not recorded because they were concentrated on or near the walls and bottom of the tank, but records were kept of the numbers added to the tank. Details regarding the feeding of

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TABLE 1.—Characteristics of five larval anchovy rearing experiments.

Experiment	1			2			3			4			5		
Number of eggs	3,000			6,000			3,000			6,000			3,000		
Temperature (±2 SE)	15.7 ± 0.21			17.7 ± 0.52			15.8 ± 0.53			15.7 ± 0.71			16.2 ± 0.33		
Percent survival[1] (age in days)	7.0 (34)			0.1 (46)			6.0 (42)			0.1 (38)			12.5 (74)		
Type additions[2]	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml	Larval age days	Numbers added/day	Mean density in tank no./ml
Millions of *Brachionus*	5-20	0.8	30	4-20	1.7	21	5-20	2.9	27	4-20	2.0	27	5-20	1.9	118
	21-34	0.5	19	21-46	0.3	8	21-42	2.3	30	21-38	0.1	19	21-74	4.0	15
Millions of *Nannochloris*	5-20	11.7	—	4-20	28.6	—	5-20	36.4	—	4-20	26.0	—	5-20	36.4	—
	21-34	14.3	—	—	—	—	21-42	7.8	—	21-38	20.8	—	21-74	11.7	—
Millions of *Artemia* nauplii	24-34	0.3	1	19-46	0.7	10	—	—	—	—	—	—	48-74	1.6	2
Thousands of *Tisbe*	—	—	—	—	—	—	—	—	—	12-20	180.0	—	6-20	260.0	—
	—	—	—	—	—	—	—	—	—	21-38	200.0	—	21-48	300.0	—
Thousands of *Artemia* adults	—	—	—	—	—	—	—	—	—	—	—	—	66-74	12.0	—

[1] Mortality includes 15 larvae removed on alternate days for length measurements.

[2] Forty liters of *Gymnodinium*, 1,700 cells/ml, were added at hatching in all groups.

anchovy larvae on *Tisbe* will be given in a separate section.

To obtain growth rates, 15 or more larvae were removed every other day from each tank, then measured, rinsed in distilled water, dried, and weighed in groups of 15.

CULTURE

Not until the fifth experiment was the procedure developed sufficiently to rear anchovy through metamorphosis. The first four experiments ended when it became obvious that it would be impossible to rear them to metamorphosis because of slow growth and high mortality. Data are included from the first four experiments to provide the background information for the final successful rearing procedure.

In all experiments, a single inoculation of 40 liters of *Gymnodinium splendens* (1,500-2,000 cells/ml) was given at age 0 days. This was sufficient to provide a final density in the tank in excess of 100 cells/ml for about 12 days. *Gymnodinium* was cultured using techniques described by Thomas et al. (1973). If fed only *Gymnodinium*, survival of anchovy larvae remains high for at least 12 days (about 45% at 12 days) but growth is depressed (Hunter in prep.).

In all experiments *Brachionus* was added on the 4th or 5th day in numbers calculated to yield a density of 30 to 50/ml in the tank (Table 1). Subsequent additions were made daily or on alternate days until day 20 in all experiments.

Nannochloris sp. was used to culture the rotifer *Brachionus* (Theilacker and McMaster 1971), and as a consequence *Nannochloris* was added to larval rearing tanks in all experiments to maintain a food supply for the rotifers. Four liters (about 13,000 cells/ml) were added on days 4 and 5, and further additions were made on the basis of water color. If water in the rearing tank was faintly green none was added as I wished to avoid creating a bloom in the tank because it is difficult to see the larvae in a dense bloom. To avoid a bloom usually required a reduction in the quantity added after 20 days. *Nannochloris* sp. is too small (about 7 μm) to be directly fed upon by larval anchovy although larvae might ingest cells accidently.

In experiments 1 and 2 *Artemia* was added at about 20 days and the level of *Brachionus* was allowed to slowly decline thereafter. In experiment 3, *Brachionus* was maintained at a high level to the end and no *Artemia* was used. Although high mortalities on the order of 30 to 300 larvae/day occurred in all three experiments between ages 20 to 30 days, the larvae in experiment 3, those fed only *Brachionus*, grew faster (Figure 1) and had a higher survival than in the two groups fed *Artemia*. From these three experiments I concluded that *Artemia* was an inadequate food for 20-day-old anchovy larvae and that growth and survival could be increased by continuing to add large quantities of *Brachionus* after 20 days. Clearly, an adequate food larger than *Brachionus* was needed for 20-day-old larvae.

The food selected was the harpacticoid copepod *Tisbe furcata*. *Tisbe* is a common contaminant in the seawater system of the Southwest Fisheries Center and can be easily reared on dried foods (Johnson and Olson 1948) or algae (DeVauchelle and Girin 1974). Copepods collected from cultures ranged from 50-μm nauplii to 1,000-μm adult females but the typical size was about 650 μm and comparable in size to *Artemia* nauplii. The first attempt to rear anchovy using *Tisbe* (experiment 4) began as the other experiments except that I began adding *Tisbe* at age 12 days at the average rate of 180,000/day. At age 20 days the rate was increased to 240,000/day and the *Brachionus* was allowed to decline. The larvae fed on *Tisbe* but growth was slow and survival low. The low survival was attributed to an insufficient number of *Tisbe* in the tank, failure to maintain *Brachionus* at a high level after 20 days, as I had in experiment 3, and too high an egg stocking density (6,000 eggs).

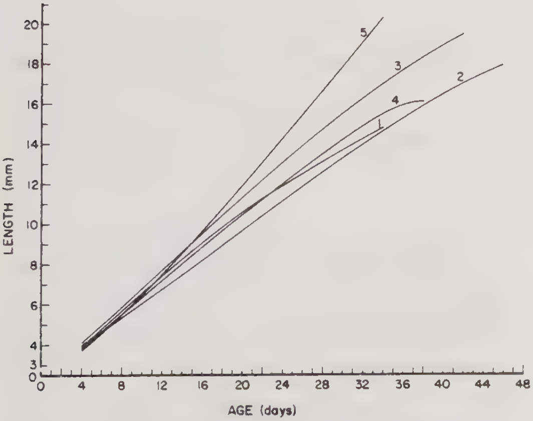

FIGURE 1.—Laird-Gompertz growth curves for lengths of anchovy larvae in five rearing experiments. Growth equation given in text; parameters for equation in Table 2. (Foods used in experiments 1-5 in Table 1.)

The first four experiments established the guidelines needed for experiment 5, the final and successful rearing experiment. Over the first 20 days *Brachionus, Nannochloris,* and *Gymnodinium* additions were managed in the same way as in experiment 3. After 20 days, additions of *Brachionus* were increased above that used in experiment 3 and maintained at a high level until the end of the experiment on day 74. *Tisbe* additions were begun at age 6 days at an average rate of 260,000/day and increased to 306,000/day after 20 days. These additions were begun before most larvae were capable of feeding upon them in order to bring the copepod density in the tank to a high level at the time feeding on *Tisbe* became common (about age 12 days, anchovy length, 7-8 mm). This procedure is practical because survival of *Tisbe* in the tank is high and consequently, uneaten animals accumulate. *Tisbe* additions ended at age 48 days (26 mm) because the quantities needed exceeded the capacity of my cultures. Although younger larvae did not survive on a diet of *Artemia* nauplii it seemed possible that larvae 26 mm long might survive because they have a differentiated digestive tract, not simply a straight tube as do younger larvae, and they have a larger gut capacity (C. O'Connell, Southwest Fisheries Center La Jolla Laboratory, pers. commun.) Rosenthal (1969) showed that *Artemia* nauplii in the guts of herring larvae were only partially digested whereas digestion of copepods was nearly complete. From this he concluded that poor survival of herring fed *Artemia* could be attributed to digestive inefficiency. Past experience in maintaining adult anchovy at the Southwest Fisheries Center showed that they survived on *Artemia*; thus, it seemed reasonable that this might first occur when the digestive tract became differentiated. For these reasons I decided to change from a diet of *Tisbe* and *Brachionus* to one of *Artemia* nauplii and *Brachionus* at age 48 days. The change from copepods to *Artemia* nauplii did not cause a noticeable mortality nor a change in growth rate. Adult *Artemia* were added at age 69 days as some of the fish had metamorphosed and readily ingested adult *Artemia*.

In this description of culture I have stressed additions rather than density of food in the tank because I felt they provided a more reliable outline of culture procedures. Density in the tank was measured before food was added and served as a guide for the quantity of food to be added. Where losses from ingestion or other sources of mortality were high, the density measurements tended to be lower than the level we attempted to maintain. In experiment 5 we attempted to maintain the density of *Brachionus* between 50 and 100/ml and that of *Artemia* nauplii at 2 to 3/ml.

In all experiments, 15 or more larvae were removed on alternate days and consequently, survival estimates include the effect of this sampling. In experiments 1 to 4 no daily counts of dead larvae were made until heavy mortalities occurred after age 20 days. In experiment 5, daily records of dead larvae were begun at age 54 and continued to the end of the experiment (age 74 days). At age 54 days 20% of the larvae were alive and at age 74 days, 374 larvae or 12.5% were alive. If the tank had not been sampled survival would probably have been greater because between 54 and 74 days the number of larvae sampled, 151, exceeded the number that died in the tank, 70. A total of 387 larvae were removed during the experiment. A method exists for estimating mortality in rearing work independent of the effect of sampling (Laurence 1974) but the programming effort required seems unwarranted for the objective of this paper. Collision with the walls of the container was a frequent cause of mortality over the last 3 weeks.

A survival of 12.5% at 74 days contrasts sharply with the other four experiments where nearly all larvae died by 30 to 40 days. Prior to the study described here, marked mortalities were common after 20 days and in all of the attempts *Artemia* was used as food. The pattern had become so typical at this laboratory that we have called it the "*Artemia* syndrome" for some years. The results of the current study suggest that the cause of the *Artemia* syndrome may simply be an inability of young clupeoid larvae with straight tube digestive tracts to digest *Artemia* nauplii but that *Artemia* may be used once the gut becomes differentiated.

It is important to call attention to the fact that 6% of the anchovy larvae in experiment 3 were able to survive for 42 days on a diet of only *Brachionus*. Plaice, *Pleuronectes platessa*, larvae have been reared through metamorphosis on only *Brachionus* although growth was slower than that on *Artemia* nauplii (Howell 1973). Howell found that plaice larvae, immediately prior to metamorphosis (12.7 mm), consumed 1,400 rotifers per day. In experiment 3, at age 42 days, the mean length of the anchovy larvae was 21.6 mm and dry weight was 5.5 mg. Assuming a digestive efficiency of 100%, larvae of this weight would have to ingest about 3,800 rotifers per day to meet metabolic requirements (calculation based on caloric value of *Brachionus* and anchovy respiration data given by Hunter 1972). These results illustrate the value of maintaining a high density of rotifers in culture containers long after a larger food has been added. They also suggest that some fish larvae have the ability to ingest large quantities of small prey and this could be of considerable benefit under natural conditions.

TISBE FURCATA AS A FOOD FOR LARVAL FISH

The evidence for the use of *Tisbe* as a food for rearing larval anchovy to metamorphosis is a single rearing experiment. It would be preferable to have additional experiments but none are planned at present because current work is concerned with only young stages and other species. Two groups of Pacific mackerel, *Scomber japonicus*, have been reared to metamorphosis using *Brachionus* and *Tisbe* as foods and this supports the contention that *Tisbe* is a satisfactory food for pelagic marine fish larvae. The work on *Scomber* will be reported at a later date.

That larval anchovy ate *Tisbe* is supported by records of stomach contents of larvae examined during the course of the rearing work. Seventy-four percent of the stomachs examined in experiment 5 contained only *Tisbe* or *Tisbe* and *Brachionus* and 26% contained only *Brachionus* (N = 69, larval length = 8.6-18.8 mm). The number of *Tisbe* in stomachs of larvae increased from 2.8 per larva (5.6-8.5 mm) to 18 per larva (17.6-20.5 mm). (Data from experiments 4 and 5 combined—Table 2.) The average length of the

TABLE 2.—Number and mean length of *Tisbe furcata* in the stomachs of anchovy larvae in experiments 4 and 5.

Larval anchovy		*Tisbe* in stomachs		
Length class (mm)	Number	Total	Number per larva[1]	Mean length μm ± 2 SE
5.6- 8.5	12	34	2.8	506 ± 57
8.6-11.5	25	90	3.6	681 ± 28
11.6-14.5	16	102	6.4	714 ± 28
14.6-17.5	9	98	10.9	758 ± 32
17.6-20.5	3	54	18.0	734 ± 43

[1] Includes only larvae that had either *Tisbe* and *Brachionus* or only *Tisbe* in stomachs.

copepods ingested by larvae also increased with larval length as expected (Arthur 1956).

Tisbe occurred throughout the rearing tank but the greatest concentrations occurred on or near the walls and on the bottom. Free swimming copepods were plentiful near the walls of the tank because *Tisbe* frequently leave the wall for short periods. Anchovy larvae captured *Tisbe* that were on the walls as well as free-swimming individuals. A pelagic copepod would be preferable to one that prefers surfaces such as *Tisbe furcata* but I have not been able to culture pelagic species in sufficient quantities for rearing work.[2]

GROWTH

The length data from each of the five experiments were fitted to the Laird-Gompertz growth equation (Laird et al. 1965) using Marquardt's Algorithm for fitting nonlinear models (Conway et al. 1970). The equation for length was:

$$L = L_0 e^{K_L(1 - e^{-\alpha t})}$$

where L = standard length in millimeters
L_0 = initial length at time 0
$K_L = A_0/\alpha$
A_0 = rate growth at time 0
α = rate of decay of growth.

A fit of the weight data from experiment 5 was also made to the Laird-Gompertz equation:

$$W = W_0 e^{K_W(1 - e^{-\beta t})}$$

where W = dry weight in milligrams
W_0 = initial weight at time 0
$K_W = B_0/\beta$
B_0 = rate growth at time 0
β = rate of decay of growth.

The length-weight relationship for larvae in experiment 5 was derived from the above two equations by James Zweifel (Southwest Fisheries Center) and had the form

$$\ln W = \ln W_0 + K_W \left[1 - \left(\frac{K_L - \ln (L/L_0)}{K_L}\right)^{\beta/\alpha}\right]$$

The Laird-Gompertz equation gave an excellent fit to the growth in length and in weight and to the length-weight relationship (Figures 2-4, Table 3). The curvilinear nature of the length-weight data evident in the log-log plot (Figure 4) clearly indicates that a linear fit to log of length and weight would lead to inaccurate estimates.

The growth of anchovy larvae in experiment 5 was about the same as that recorded by Kramer and Zweifel (1970) for anchovy fed wild plankton at 17°C. At age 34 days, the last day of their experiment, the mean length of larvae was 17.4 ± 1.8 mm and that in experiment 5 at age 34 days was 19.7 ± 1.0 mm. Thus, over at least the first 34 days, growth on the cultured food diets was about the same as that on wild plankton.

SURVIVAL AT METAMORPHOSIS

The object of this experiment was to determine how long newly metamorphosed anchovy larvae can survive without food. Most adult fishes and presumably the anchovy can withstand prolonged periods of starvation of weeks or months. On the

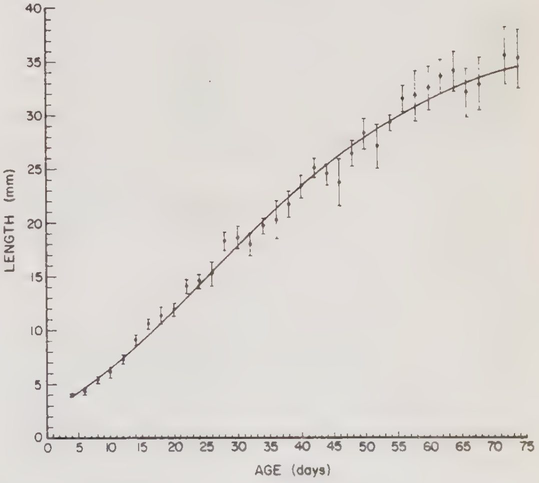

FIGURE 2.—Laird-Gompertz growth curve for length of anchovy larvae in experiment 5 and mean length ± 2 SE. Parameters for equation given in Table 2.

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[2] At present our copepod culture system is composed of 10, 90-liter, glass, rectangular tanks maintained at 17° to 19°C. The *Tisbe* are given green algae, either *Tetraselmis* or *Nannochloris*, which is grown using commercial plant fertilizer (fish emulsion). An inoculation of 50,000 to 100,000 copepodid-adult stages yields on the average 500,000 copepods in these stages in 2 weeks. A tank is drained, harvested, and reestablished 5 days a week producing about 2.5 × 10^6 copepodid-adult stages per week, which is sufficient to rear one group of anchovy in the manner described. Occasional harvests of over a million in 2 weeks have been obtained suggesting that major improvements in the technique are possible. Contamination by *Brachionus* has been a problem because it increases the amount of algae that must be added to the culture. A more detailed description of this culture system would be premature but a description of a similar method of mass culture exists (DeVauchelle and Girin 1974).

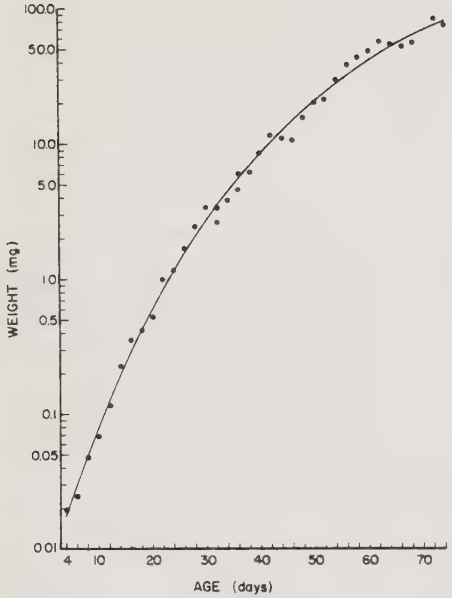

FIGURE 3.—Laird-Gompertz growth curve for dry weight of anchovy larvae in experiment 5. Points are average weight of larvae weighed in groups of 15-26 larvae each. Equation for curve given in text; parameters for equation in Table 2.

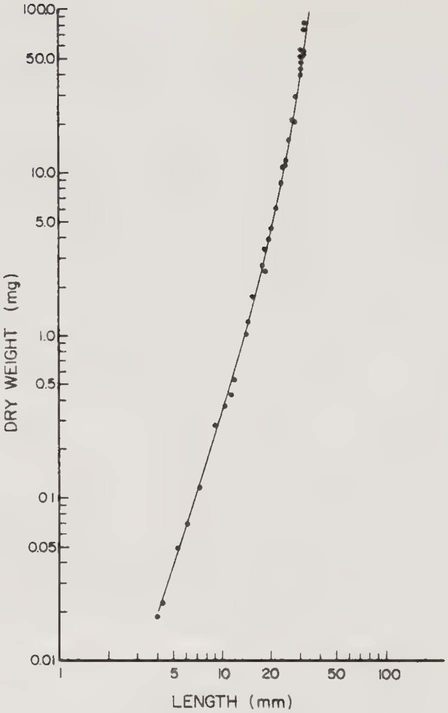

FIGURE 4.—Length-weight relationship of anchovy larvae reared in experiment 5. Equation for curve given in text; parameters for equation in Table 2.

other hand, larval anchovy, after they absorb their yolk, survive only 1 to 2 days without food (Lasker et al. 1970). The point at which this extreme vulnerability to starvation ends is essential information for any model of anchovy ecology and survival.

In this experiment fish reared to metamorphosis in experiment 5 were used. At age 74 days a group of 53 fish (group 1) and one of 73 (group 2) were placed into tanks containing only filtered seawater and a sample of 29 fish was taken for length and weight measurements. The tanks were the same as those described for the rearing experiments and temperature was maintained at 16°C. *Artemia* nauplii were offered to group 1 after 12 days of starvation and to group 2 after 15 days; the experiment ended after 20 days. Daily records were kept of water temperature and lengths of dead fish; after 20 days all surviving fish were measured. Total lipid content was also monitored through the course of the experiment.

TABLE 3.—Parameters and 95% support plane[1] for Laird-Gompertz growth equation for length, experiments 1-5, and weight for experiment 5. Symbols and equations are given in text.

	L_0			A_0			α			
		Support plane			Support plane			Support plane		
Experiment	Parameter	Lower	Upper	Parameter	Lower	Upper	Parameter	Lower	Upper	Number of observations
Length										
1	2.4378	2.0856	2.7901	0.1349	0.1040	0.1658	0.06939	0.05366	0.08512	289
2	3.0600	2.5512	3.5688	0.0835	0.0614	0.1056	0.03936	0.02700	0.05171	358
3	2.8361	2.3894	3.2829	0.1088	0.0835	0.1342	0.04951	0.03696	0.06206	345
4	2.6711	2.1648	3.1774	0.1098	0.0792	0.1404	0.05185	0.03591	0.06779	345
5	2.4928	2.2219	2.7636	0.1167	0.1042	0.1292	0.04264	0.03865	0.04663	553
	W_0			B_0			β			
Weight										
5	0.005758	0.003046	0.008470	0.2997	0.2552	0.3442	0.02725	0.02243	0.03206	35

[1] An approximation of the 95% confidence limits (Conway et al. 1970).

Fat was removed by Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950) from batches of 5 to 9 fish each. One such sample was taken at the beginning of the experiment, one from each group just before food was added, and one from each group when the experiment ended after 5 to 8 days of feeding.

A marked initial mortality occurred on the day following the transfer of the two groups (Figure 5) which was probably caused by handling. For this reason the first day's mortality is excluded from the analysis presented below, but the survival is given for all days in the figure.

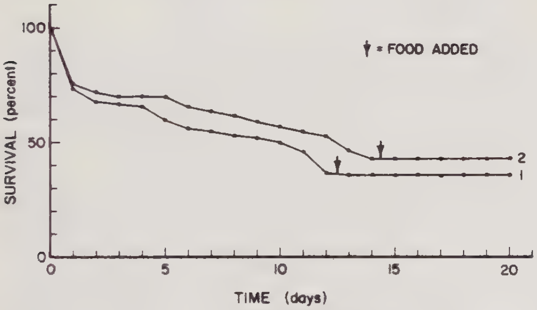

FIGURE 5.—Percent survival of metamorphosed larvae reared in experiment 5 during starvation periods of 12 and 15 days. Arrow indicates end of starvation period.

TABLE 4.—Lengths of fish in starvation groups and lengths of fish that died during starvation.

Group	Number of fish			Percent	Mean length
	Length <35 mm	Length ≥35 mm	Total[1]	<35 mm	mm ± 2 SE
Sample before starvation	13	16	29	45	35.4 ± 1.8
All fish[2]:					
1	29	25	54	54	34.4 ± 1.5
2	16	24	40	40	36.0 ± 1.7
1 + 2	45	49	94	48	35.1 ± 1.1
Dead fish:					
1	21	4	25	84	30.9 ± 1.4
2	14	3	17	82	31.8 ± 1.6
1 + 2	35	7	42	83	31.2 ± 1.1

[1] Fish that died on first day of starvation in groups 1 and 2 not included.
[2] Surviving fish measured at end of experiment after 5- to 8-day feeding period.

After 12 days of starvation, 50% of the fish were alive in group 1 (excluding the first day mortality) and 58% were alive in group 2 after 15 days of starvation. One fish in group 1 died the day after the first feeding. This was the only fish to die after feeding began. Thus for fish averaging 35 mm in length, about 50% mortality is reached after about 15 days of starvation and nearly all surviving fish are able to recover from a starvation period of that duration. Mortality during starvation appeared to be dependent on size or state of maturity, however. Metamorphosis is completed in the northern anchovy when they reach 35 mm standard length (E. H. Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, pers. commun.). Eighty-three percent of the fish that died were less than 35 mm whereas only 17% of those longer than 35 mm died (Table 4). About 45% of the fish were less than 35 mm long at the beginning of the experiment. These results are similar to those obtained for herring larvae, *Clupea harengus*. The number of days to irreversible starvation for herring larvae increased from 6 days at the end of the yolk-sac stage to 15 days at age 88 days (Blaxter and Ehrlich 1974).

Lipid content of fish declined during the starvation period from about 30% of dry weight to about 12% (Table 5). Recovery for the surviving fish was rapid, as they returned to the 30% level after 5 to 8 days of feeding. Water content was inversely related to fat as expected (Iles and Wood 1965). Fat content of muscle of adult anchovy is about 30 to 40% of dry weight during late summer and fall when gonadal fat is low (Lasker, Southwest Fisheries Center La Jolla Laboratory, unpubl. data). Thus, fat levels of these newly metamorphosed larvae appeared to be about the same as that of adult fish.

TABLE 5.—Total lipid and water content of anchovy at metamorphosis before, during, and after starvation.

Treatment	Elapsed time (days)	Water (%)	Total lipid dry wt (%)	Dry wt (mg)	Mean length (mm)	*N*
Before starvation	0	78.1	30.6	74.6	35.0	7
End starvation:						
Group 1	12	83.2	10.5	33.3	32.8	7
Group 2	15	82.9	13.4	54.2	36.9	5
End feeding:						
Group 1	20	79.5	32.3	90.3	39.6	9
Group 2	20	79.2	32.3	83.7	39.8	6

Extreme vulnerability to starvation appears to be characteristic of only the larval phase of the northern anchovy and it is over by the time the fish completes metamorphosis. There is a danger in interpreting these data beyond these general conclusions because reared fish may have more fat than wild ones and this could alter the results (Balbontin et al. 1973).

ACKNOWLEDGMENTS

James Zweifel (Southwest Fisheries Center La Jolla Laboratory) fit the Laird-Gompertz growth equation to the data and derived the length-weight relationship from the growth equations. Carol Sanchez (Southwest Fisheries Center La Jolla Laboratory) assisted in all phases of this work. Reuben Lasker and Gary Stauffer (Southwest Fisheries Center La Jolla Laboratory) reviewed the manuscript.

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Report of a Colloquium on Larval Fish Mortality Studies and Their Relation to Fishery Research, January 1975

JOHN R. HUNTER, Editor[1]

ABSTRACT

One of the critical problems in fishery research today is the inability to determine how the abundance of adult fishes affect the strength of incoming year classes. The report summarizes the discussions of experts on how studies of larval fish mortality may assist in solving this problem. Included in this report are discussions of the principle causes of larval mortality and their possible relation to stock size. Guidelines and recommendations are made regarding future research on the mortality of larval fish.

INTRODUCTION

One of the critical problems in fishery research today is our inability to determine how the abundance of the adults affects the strength of incoming year classes. Thus, the management strategy that should be adopted to ensure good recruitment is unknown. Relating recruitment to parent stock seldom gives useful answers even when many years' data are available. It was agreed that a precise determination of the stock-recruitment relation earlier in the life history lies in a better understanding of mortality and growth in the larval stage.[2]

Similarly, the factors which maintain the stock within the observed limits or which cause the occasional and remarkable rises or falls in population (e.g., the collapse of the Pacific sardine populations), as well as many of the critical aspects of competition between species, also appear to have their effect in the first year of life. Neither those changes in growth nor those in natural mortality, which occur after recruitment, are sufficient to be controlling factors. Studies of larval mortality appear to hold the key to determine the factors controlling the fate of fish populations.

On the other hand, it appears unlikely that it will be practical to use the results of larval counts and measurements to provide timely estimates of year-class strength. Several other methods may be available for early estimation of year-class strength, including commercial catches of very small fish, and trawl or acoustic surveys on different sizes of fish. The choice among these will be determined by the costs involved, the general variability of year classes in the stock, and the timeliness and accuracy required. It appears that the high costs and time delays in processing catches of larval fish to provide estimates of year-class strength are reasons for using alternate methods to determine year-class strength. However, for species that have a distribution greater than the range of the fishery, or for those where no commercial fishery exists, the best available method for estimating abundance is the egg and larval survey even with its inherent limitations.

The importance of the stock-recruitment relation and the difficulties in solving it suggest that as long as larval mortality studies offer some reasonable chance of resolving the problem they should be actively pursued. However, no certainty exists that larval mortality studies will, in any reasonable time, resolve the stock and recruitment problem in a fully satisfactory manner. Attention needs to be concentrated on differences in larval mortality rates between high and low adult densities, between years resulting in good and bad year classes, and between areas of better or worse larval survival.

The work required includes the estimation of larval mortality at sea under different conditions of food and stock; construction of models to simulate larval mortality with limits set on food, predation, and stock; and laboratory and field experimentation designed to estimate the parameters needed for the models. Although it is important to treat the problem of stock and recruitment in a holistic fashion, it is unlikely that any new general models can be formulated at the present time. Variables requiring detailed examination are likely to differ from stock to stock. Similarities may exist within systematic groups, for example in codlike fishes or within excological associations, such as that of Pacific sardine, *Sardinops sagax* (Jenyns), and northern anchovy, *Engraulis mordax* Girard; but even here, differences in seasonal phenomena, such as time of spawning, may require different approaches.

CAUSES OF MORTALITY

It is our opinion that the major causes of larval mortality are starvation and predation, and that these may interact. Larval research has been weighted toward studies on food, feeding, and starvation in fish larvae. Relatively little work has been done on predation. We believe that effort should be directed to studies of the relative importance of starvation and predation and, in some cases, other possible sources of larval mortality, such as disease, parasites, pollutants, turbulence, transport, and mechanical damage.

The number of eggs per female, as well as quality of eggs (biochemical content, size, and genetics) may also be important. In a given species, e.g., the Atlantic herring, *Clupea hargengus harengus* Linnaeus, fecundity and egg size are inversely related, hence if a large number of eggs is produced, the average egg size is small and the average time to starvation of larvae will be shorter. Field studies on the fecundity-egg size relation would appear not to have immediate utility in relation to density dependence.[3] On the other hand, the number of eggs spawned per female can be influenced by abiotic factors, such as temperature. Temperature can influence onset of spawning and even the duration of the spawning season; in the 1950's this was true for the Pacific sardine. Temperature may control the number of eggs that could be matured and spawned and therefor influence recruitment.

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[2] All stages between egg and recruitment would be interesting to investigate and may have importance in the stock and recruitment relation. However, this Colloquium has focused primarily on the contribution of studies of the larval stage.

DENSITY-DEPENDENT MORTALITY

The principal concern of larval fish studies should be to study the density-dependent aspects of starvation and predation because these aspects of mortality, we believe, will provide the understanding of the stock and recruitment relation. To determine density-*dependent* mortality one must either measure it directly or measure density-*independent* mortality and subtract it from total mortality. To separate density-independent mortality from density-dependent mortality is probably not possible at present. Nevertheless, some possible density-dependent mechanisms for starvation and for predation are described below.

Mechanisms of Density-Dependent Mortality Caused by Starvation

Three density-dependent mechanisms relating to starvation are 1) intraspecific competition for food, 2) increases in adult population that lead to the expansion of spawning into areas where the probability of concentrations of food suitable for larval survival are very low or nearly nonexistent, and 3) interspecific interactions.

Intraspecific Competition for Food.—The spawning behavior of the adults must be understood before considering the intraspecific competition of larvae for food. In demersal spawners, the density of spawn in a patch may be a function of population size and an increase in population size may lead to increased spawning intensity within the optimal habitat rather than an increase in the breadth of the spawning area. On the other hand, in pelagic spawners, a possible result of an increase in size of the spawning population is an increase in the size or number of patches of eggs and larvae rather than a higher density of eggs or larvae within a patch. Thus, population size may not control the outcome of intraspecific competition within the patch of first feeding larvae of pelagic spawners. Intraspecific competition for food that produces a density dependent mechanism could occur after the larvae begin schooling and consequently become aggregated. By this stage, the larvae have a greater food storage capacity, greater body reserves, and increased speed so that their susceptibility to starvation is less than that of younger stages.

Expansion of a spawning population.—The second mechanism considered here is the expansion of a population and consequently its spawning activity into less suitable areas. The tacit assumption in this mechanism is that at lower population levels, the boundaries of the spawning population become confined to an area where the long-term probability of the larvae finding food is greater. Two density-dependent mechanisms relating to food can be proposed depending on the characteristics of the area to which the species becomes confined under lower population levels. One such area could be relatively large geographically, where survival depends on coincidence of larvae with concentrations of food (patches) that are highly unstable and vary greatly in space, annually, and within a season. The alternate possibility is that within the typical spawning area of a species there exists a limited area that consistently produces suitable concentrations of food throughout the spawning season and from year to year. This area would be a relatively stable food enclave that is consistently used for spawning. One can conceive of many intergradations of these two extremes, but the important point is that each would produce different mechanisms relating to starvation, and the problem of starvation and density dependence should be examined in this context.

Interspecific competition.—Starvation mechanisms must be viewed in the context of possible interspecific interactions. The enclave mechanisms described in the preceding section could lead to more intense interspecific competition between ecologically similar species,[4] e.g., the anchovy and sardine. If at low population levels, a population spawns principally in a small consistently favorable forage area, it might be expected that the eggs and larvae of ecologically similar species might also be concentrated in that area, and consequently the likelihood of competition for food increases. Population changes may also be mediated through rather subtle interspecific interactions. For example, an infrequent, unbroken series of years disadvantageous to any two species might exceed the longevity of one species but not the other, allowing the latter species to achieve subsequent dominance by reproduction of the survivors.

Knowledge of which mechanisms are important for a species would require measurements of the distribution of patches of eggs, larvae of all species at the same trophic level, their food, and determination of the persistence of these patches within a season and from season to season. The approach used to collect these data would differ depending on the hypotheses to be tested. Intensive field work over a limited area would be required for the enclave work whereas extensive rather than intensive field work would be required for the mechanisms involving large geographic areas.

Mechanisms of Density-Dependent Mortality Caused by Predation

Predation on larval fishes that could produce density-dependent effects include: cannibalism by adults; reproductive response of a predator population to the production of eggs and larvae; attraction of predators as a function of the size or density of patches of eggs or larvae; selection of prey by the predator as a result of experience; and survival of the predator as a function of the abundance of eggs or larvae.

Predators could be planktonic or nektonic. The latter, such as fish, could aggregate in patches of larvae or eggs by kinetic mechanisms such as changes in swimming speed or frequency of turning which could be a function of the size or density of patches of larvae or eggs. Planktonic predators may select eggs or larvae as the result of past experience. There also may be a minimum quantity of larvae needed to elicit selective predator response.

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[3] Some members of the Colloquium believed that critical studies on the fecundity-egg size relation need to be done on a population basis.

[4] Researchers should recognize that some species may compete only during the larval stage.

To evaluate the reproductive response of a predator to eggs or larvae, the duration of spawning of the prey must be considered. In subarctic areas where the spawning period is short, there may be little time for a predator to specialize on any particular developmental stage of the fish population. On the other hand, in the tropics where spawning often is continuous, a predator could specialize on a particular developmental stage and predators with long generation times could cause density-dependent mortality of larvae. Predators could also produce density-dependent effects through changes in their survival rate. The response of a predator population to an abundance of eggs and larvae could be decreased mortality from starvation. Hence, the predator could have a potentially greater impact at high population levels of eggs and larvae than at lower levels.

GUIDELINES FOR THE STUDY OF STARVATION

Certain laboratory studies are essential for an understanding of stavation as a cause of larval mortality. They are needed to interpret field data and to identify parameters and their range of values. The committee suggests the following kinds of laboratory studies, not necessarily in order of priority:

1. A study of the feeding strategy of larvae to determine patterns of activity, feeding, aggregation mechanisms, search patterns, and prey selectivity.
2. Studies of effects of temperature to determine hatching times and developmental rates and to know when larvae require food.
3. Studies of larval fish energetics that allow one to specify the concentration sizes and nutritional content of food particles required for maintenance and growth.
4. The determination of digestion, assimilation, and food conversion rates.
5. Establishment of anatomical, histological, biochemical, or physical criteria that indicate larval starvation or viability.
6. A study of the development of sensory and motor capabilities of larvae.
7. The study of egg-size distribution within a species and its effect on larval size, early swimming ability, size of potential prey, and resistance to starvation.
8. The study of the relation between a larva's ability to avoid predation and its physical condition and size.

Many of these studies have been done for some of the more frequently studied and cultured marine fishes, e.g., plaice (*Pleuronectes platessa* L.), northern anchovy, and Atlantic herring; but in no species is all this information complete. On the other hand, attempts to relate these laboratory findings to field conditions are rare. We believe, therefore, that the most critical areas in the study of starvation as a cause of mortality are transitional studies that bridge the gap between laboratory and sea work. Three approaches exist: 1) application of laboratory results to the field situation; 2) development of new experimental techniques that can be used at sea; and 3) development of new mathematical models from existent laboratory and field data.

Development of models to relate laboratory studies to starvation at sea are greatly hindered by the lack of adequate information on the abundance and spatial and temporal distribution of food of the appropriate size for fish larvae. Few studies of this kind exist and there is an urgent need for this information before realistic models can be developed. These models should point out where there are critical gaps in our knowledge and thus provide a guideline for future studies. Where studies exist, data seem to indicate that the average density of food in the sea is often insufficient to provide a larva's daily requirement. When the average density of food is less than a larva's daily requirement, it becomes advantageous to larvae for food to be distributed in patches. Thus, it appears that the patchiness of food may be a factor that reduces larval starvation. For this reason, we shall deal separately with the problem of patchiness of food and then consider transitional field studies.

Patchiness of Food and Larvae

Patchiness of larvae and their food must play a crucial role in survival. Confusion exists in the terminology used to describe patchiness. Patchiness may be examined at various spatial levels which need to be accommodated within existing descriptions. Patches may range from tens of kilometers, large enough to be sampled and studied conveniently, to patches equivalent to the perceptive field of the organism or its cruising range. The latter category could vary with organism size; for example, the patches of larval food could be measured in meters, patches of larvae in tens of meters, and patches of their predators in hundreds of meters.

The factors associated with patchiness of phytoplankton and zooplankton include nutrient distribution and diffusion, light penetration, growth and reproduction, and the presence of strata of food organisms as well as the swimming kinetics of some food organisms. Patches of eggs and larvae could be caused by spawning habits of the parents, selective survival of larvae, kinetic mechanisms of larvae, and schooling or other social behaviors of larger larvae. Kinetic mechanisms that could produce patchiness of larvae are motor patterns that result in larvae finding and remaining in areas where they find food. This mechanism may be significant only on a small scale whereas patchiness produced by selective survival, that is, patterns of larval distribution produced by discontinuous areas of survival and mortality, might be evident only on a much larger scale. Larval schooling could produce patchiness, but in many epipelagic larvae, schooling develops late in larval life and consequently would be of greater significance to juvenile survival.

Variables that could cause dispersion of larvae and their food include: wave-induced turbulence, wind-induced shear, upwelling, tidal currents, and eddies of various time and space scales. Dispersion of patches can best be studied by measuring changes in the distribution of the organisms and not by measuring the continuous characteristics of physical and chemical factors of seawater.

Scale, persistence, and other characteristics of patches of larvae and their food should be studied. It should be recognized, however, that such work should be considered as a first step in the broader objective of obtaining time series data showing the changes in patchiness from season to season or from year to year. Recent observations indicate that the relation between persistence of patches and abiotic factors, such as wind strength, should be investigated.

Transitional Field Studies

In this section, six types of field studies will be considered that should help relate laboratory to field studies on starvation as a cause of mortality.[5] Each is considered separately below.

1. **Assessment of age of larvae in the sea.** A critical problem in larval mortality studies is the assignment of absolute age to larvae collected at sea. The ability to age sea-caught larvae in increments of a day or several days would greatly facilitate estimates of mortality and other life history parameters. It is particularly important to evaluate growth in terms of temperature and food availability. Aging may possibly be done using size and morphological characteristics corrected for temperature in selected species. More general means must be sought for other species. A promising technique is the use of otoliths for measuring daily growth increments. This technique should be explored intensively to ascertain how early a valid age determination can be made. Other age determination techniques also need to be developed.

2. **Bioassay experiments.** In these studies, laboratory spawned larval fish are used in shipboard feeding experiments designed to determine if water from a particular location and depth in the sea is suitable for larval survival. Owing to possible differences between laboratory-reared and wild larvae, these experiments may have to be confined to younger larvae. Work of this kind is already under way at several laboratories (Bergen, Norway; Brookhaven National Laboratory; Southwest Fisheries Center, U.S.A.), and it seems to be a useful method for determining suitable areas and depths of larval food and for estimating patchiness.

3. **Assessment of starvation in the sea using net-caught larvae.** In these studies, criteria are developed in the laboratory to identify starving larvae, using anatomical, biochemical, or other criteria. Net-caught larvae can then be examined using these criteria to determine the incidence of starvation or general health of the larvae. Work of this type is under way in several laboratories (Dunstaffnage, Scotland; Southwest Fisheries Center) and seems promising.

4. **In situ growth and mortality experiments.** In these studies, larval fish are placed or entrapped in an enclosed or partially enclosed volume of water at sea, and mortality and growth measured over a period of days or weeks. A completely enclosed container, like the plastic bag experiments of the past, could be used; or a cylinder could be provided with a bottom that can be pursed. In the latter case, the depth of the cylinder would have to exceed the vertical migrating tendencies of the larvae. To assess density-dependent mortality, different stocking densities of larvae could be used. Predation could possibly be simulated by use of a plankton net. Such experiments with larval fish are untried and the panel was not in general agreement on the value of such an approach.

5. **Following cohorts of larvae at sea.** It is proposed that a cohort of larvae or group of cohorts could be followed to record growth, estimate mortality, and estimate abundance of food and predators. This technique allows multiple pairs of observations of mortality and other parameters to be obtained from each spawning cohort. Plaice larvae in the southern North Sea form clearly recognizable patches that have been followed for 10 to 20 days. The continued identity of plaice patches is ensured by the complete vertical mixing in this area. Elsewhere, shears at different water depths could break up identifiable patches. It might also be possible to choose an area without a patch and to follow the population of larvae through that region; but this approach would be practical only if the initial spawning is limited in area and time.

6. **Coincidence of larvae and their food.** Many plankton surveys in the past have not sampled the micro-zooplankton which is eaten by fish larvae. It is important that such surveys be made so that the coincidence of larvae and food of the appropriate size can be determined. The scale of sampling is an important consideration of this work, because scale must be considered in terms of larval behavior and the patchiness of the food. Systematic work on the naupliar and copepodid stages must be encouraged as the early stages of many important species cannot be identified. Work on the production of biomass for these stages must also be done.

GUIDELINES FOR THE STUDY OF PREDATION

Predation studies have been so neglected that it is difficult to specify in detail the work that needs to be done. Indeed, the brevity of the following section reflects the paucity of knowledge. We believe that predators need to be identified; their co-occurrence with larvae and eggs, their abundance in time and space, their feeding strategy, and their ability to capture different life stages need to be determined. It is of major importance in any study of predation to examine the possible interactions between starvation and predation. Clearly, if slower growing larvae and larvae weakened by starvation are ingested much more frequently than healthy ones, the controlling mechanisms must be sought in food abundance rather than in predation alone. It is also of major importance that density-dependent mechanisms, such as those described in preceding sections (e.g., cannibalism, reproductive response, and other responses by predators) be evaluated.

Hypotheses on the nature of larval predation should be tested by appropriate analyses of past data and specially designed studies. As a first step, potential predators must be identified by examination of their gut contents. Residence time of eggs and larvae in their intestines should be determined. Predators may be identified by observing aggregations of potential predators in areas where spawners, eggs, larvae, or later stages are congregated. Potential predators may also be identified by analysis of the abundance and co-occurrence of possible predators with eggs and larvae from ichthyoplankton survey collections and other survey data. In concert with field studies, laboratory experiments should be done on the effect of larval size, larval condition, predator search patterns, and feeding behavior on the degree of predation. Laboratory studies should also be done on larval avoidance mechanisms, recovery from predatory attack, and residence times of identifiable eggs or larvae in guts of predators. Once predators are identified and their predatory potential evaluated, sea studies should be made to determine density and distribution of predators in relation to target species, and field models of predation (e.g., an encounter model) should be developed.

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[5] Professor John Isaacs remains convinced that "the remarkable relationships between the numbers of day-caught and the numbers of night-caught larvae (over the properly sampled size range) of the sardine and anchovy are interpretable in terms of relative growth rate changes and relative mortality of the two larval species. These criteria, derived from the zooplankton net samples of the CalCOFI Cruises, 1951-1957, correlate closely with estimated recruitment."

RESEARCH RECOMMENDATIONS

1. We recommend that efforts be made to develop methods to directly age larvae captured at sea on an absolute time scale to confirm age determination based on length frequency. Such studies should first be carried out in the laboratory and then applied to sea-caught larvae.
2. We recommend that studies be initiated in the laboratory and at sea to assess the effect of predation on larval mortality and that interactions between starvation and predation be emphasized.
3. We recommend that work be continued on relating food supply to larval mortality. Of particular importance is the need for transitional studies that link laboratory and field studies, including estimates of the relevant microzooplankton biomass that constitutes the food of larval fishes; studies of the patchiness of food distribution in the sea and its impact on larval survival; and development of methods to determine larval viability from sea-caught specimens.
4. We recommend that simulation models of the recruitment process be developed. These models should have the following characteristics:
   a. The models must be able to account for mortality rates of the observed order of magnitude.
   b. They must be able to account for density-dependent mortality if it exists at some stage between egg and recruitment.
   c. They must be sufficiently generalized to obtain simultaneous estimates of mortality in more than one species to allow the possibility of detecting competition if it exists.
   d. Realistic variations in the basic input parameters should not generate variations in the resultant recruitment any greater than those observed in the sea.
   e. They should be biologically plausible.
5. Finally, we recommend studies of the relations between numbers of larvae alive at various stages and subsequent recruitment, in order to establish the earliest stage at which recruitment is determined. This would reduce the number of life stages needed to be studied to determine the density-dependent effects of larval and juvenile survival on the strength of future year classes.

SELECTED REFERENCES

Listed below are a selection of general references dealing with larval fish research and related fishery problems. General reference books and reports of symposia were chosen because most of the pertinent information on larval fish mortality can be found in them. In a few instances, individual research papers are given because the work was too new or was not included in one of the cited reviews.

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DIEL CHANGES IN SWIM BLADDER INFLATION OF THE LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

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ABSTRACT

Laboratory and field studies demonstrated that larval anchovy 10 mm standard length and larger inflate their swim bladders each night and deflate them in the day. Maximum night levels of inflation were attained 2 h after the onset of dark and typical day levels occurred about 2 h after the onset of light. Laboratory experiments indicated that larvae fill their bladders at night by swallowing air at the water surface and the vertical distribution of sea-caught larvae suggested that they migrate to the surface each night to fill their swim bladders. Gas is released by passing bubbles through the pneumatic duct into the alimentary canal. The diel rhythm of inflation was viewed as an energy sparing mechanism. Measurements of sinking speed of larvae with and without inflated bladders suggested that the energy saved at night by inflation of the swim bladder would exceed the cost of vertical migration to the surface and that the migratory range over which energy savings are possible would be greater as larvae increased in length.

Northern anchovy, *Engraulis mordax* Girard, are more vulnerable to starvation in the larval stage than at any other time of life, consequently, energy sparing mechanisms may be critical to their survival. In a recent paper Uotani (1973) showed that the larvae of several clupeoid fishes, *Engraulis japonicus* (Houttuyn), *Sardinops melanosticta* (Temminck and Schlegel), and *Etrumeus teres* (DeKay) have expanded swim bladders when captured at night in the sea and deflated ones when captured during the day. Energy conservation is certainly one of the possible adaptive advantages of such behavior, but the energy saved must be evaluated in terms of the energy cost of daily filling the bladder. This requires that the mechanism of filling be known. The object of the present study was to determine if the larvae of the northern anchovy display a similar rhythm and to evaluate this behavior as a possible energy sparing mechanism.

The swim bladder in adult northern anchovy is a tubular vesicle that extends the length of the body cavity. It is connected to the alimentary canal by a pneumatic duct which originates from the dorsal wall of the cardiac stomach; no anal duct exists as it does in some clupeoids (O'Connell 1955). Two tubules on each side of the body extend from the anterior end of the bladder into the cranium where they expand into two pairs of capsules, termed prootic and pterotic bullae (O'Connell 1955). The swim bladder of the larva is basically similar to that of the adult. At the time of initial filling of the swim bladder, the pneumatic duct is functional and the bullae become filled with gas. No histological evidence exists for gas secretion in adult *E. mordax* nor for the larvae (O'Connell 1955, and pers. commun.).

The swim bladder is deflated by passing gas bubbles through the pneumatic duct into the alimentary canal and out the anus. On a number of occasions we have observed this process while examining a live anchovy larva under a dissection microscope. We have also captured larvae with deflated swim bladders that had gas bubbles in the alimentary canal.

METHODS

Fertilized anchovy eggs were obtained from a captive population of adults maintained in spawning condition in the laboratory (Leong 1971) and the larvae were reared using the techniques, foods, and tanks described by Hunter (1976). The larvae were reared at temperatures of 16.5° ± 0.2°C and 16.9° ± 0.9°C. A 12-h photoperiod was used without a dawn or dusk transition in light intensity. Incident light at the surface was about 2,000 lx in the day and at night no light was provided in the closed room which contained the rearing tanks.

Larvae reared in the laboratory were sampled at

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various times of day commencing at age 1 day to determine if a daily rhythm of inflation existed and to determine the larval length at which the swim bladder was inflated. Samples of preserved specimens from California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton collections were also examined to determine if differences existed in swim bladder inflation in sea-caught specimens.

The standard length was measured to the nearest 0.1 mm and the maximum width and length of the swim bladder to the nearest 0.02 mm. The volume of the swim bladder was calculated by using the equation for a prolate spheroid, $V = 4/3\pi ab^2$, where a is half the maximum bladder length and b is half the maximum width. For larvae 16 mm and larger, the calculated swim bladder volume may be converted to actual gas volume by multiplying it by the coefficient 0.82 (Figure 1). This conversion is based on data obtained while measuring the composition of swim bladder gas. The larvae used in that experiment were larger (mean length 15.6 to 29.6 mm) than most of the larvae in the rest of the experiments. For this reason we have used the calculated swim bladder volume in all computations.

We also sampled larvae reared in the laboratory to determine the effect of swim bladder development and swim bladder inflation on sinking rate. The method of Blaxter and Ehrlich (1974) was used to measure sinking rates of larvae. Larvae anesthetized in MS 222[2] were measured and added to a 1-liter graduated cylinder without contact with the air. The larvae were allowed to sink a few centimeters, then the rate of descent was timed with a stopwatch for a distance of 7 to 35 cm. Only one measurement was made per larva and larvae were reexamined after the test to determine if they were still alive (dead larvae sank faster than live ones) and if any gas had been lost from their bladders. Fresh seawater was used in the graduated cylinder for each day's run and the specific gravity and temperature of the seawater were measured before each larva was tested. The specific gravity averaged 1.0262 and ranged from 1.0259 to 1.0266. The graduated cylinder was immersed in a temperature-controlled water bath which was maintained within 1°C of the rearing temperature. One rearing group was tested at 15.9° ± 0.2°C and another at 18.0° ± 0.1°C. In the Results section we have combined the data from these two rearing groups because covariance analysis indicated that the differences in sinking speed when adjusted for swim bladder volume and larval length were not significant.

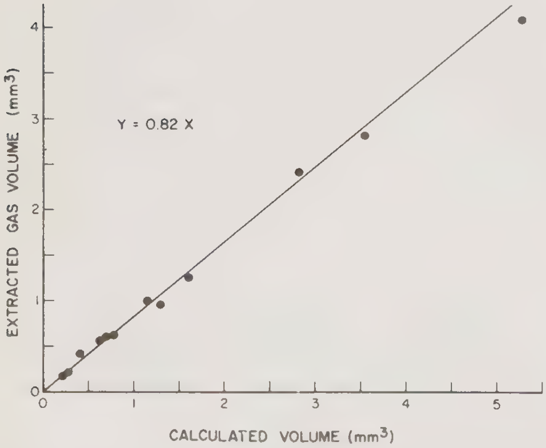

FIGURE 1.—Relation between the volume of the swim bladder calculated from the equation $V = 4/3\,\pi\, ab^2$ and the actual volume of gas extracted from the swim bladder for northern anchovy larvae of mean length 15.6 to 29.6 mm. Each point is the mean volume of the swim bladder calculated for a sample of two to eight larvae taken at night and the average volume of gas extracted from that sample. Sample means were weighted by their variances to calculate the regression line; intercept for line did not differ from 0; and the standard error of line was 0.0428.

To determine if anchovy larvae filled the swim bladder by gulping air at the water surface, the following experiment was performed. Commencing 4 h after the onset of dark, larvae in a 400-liter rearing tank were sampled and the lengths and dimensions of the swim bladder of each larva in the sample measured. Just before the onset of dark on the following day, the surface of the tank was sealed with a 0.5-cm layer of mineral oil. A second sample was taken commencing at 2400 h, 4 h after the onset of dark and ending just before the beginning of light at 0800. A third sampling was taken of larvae in the sealed tank during the day beginning at 1000 h, 2 h after the onset of light, and ending at 1400.

The gas content of the swim bladders of laboratory-reared larvae captured in the dark was analyzed using the micro gasometric method and apparatus described by Scholander et al. (1955). Swim bladders were dissected from the larvae in acid citrate solution, removed with a Pasteur pipette, and injected into an acid citrate filled capillary tube sealed at one end. After two to eight swim bladders had been collected, they were macerated in the tube and the gas withdrawn with a Pasteur pipette and inserted into the syringe gas analyzer (Scholander et al. 1955). In the analyzer, the carbon dioxide was absorbed with alkaline citrate, oxygen by pyrogallol, and the volume of gas determined before and after each treatment. The remaining gas was considered to be nitrogen. The volume of gas was read under a dissecting microscope using an optical micrometer. Reading error was about ±0.09 μl or from 1 to 2% depending on the volume of the sample.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Diel Rhythm in Swim Bladder Inflation

The volume of the swim bladder of larvae captured at night in the sea was greater than that of larvae collected in the day (Table 1). Similarly, the volume of the swim bladder of larvae reared in the laboratory was greater at night than in the day. To illustrate these daily changes for laboratory-reared larvae, the mean volume of the swim bladder for 2-h intervals was calculated for each of three length classes (10.0 to 11.9 mm, N = 121; 12.0 to 13.9 mm, N = 202; 14.0 to 15.9 mm, N = 129). No evidence existed for anticipation of the onset of dark at 2200 h nor for the onset of light at 1000 h (Figure 2). In all three length classes the mean volume did not return to the daytime level until about 2 h after the onset of light nor did they reach the maximum at night until about 2 h after the onset of dark.

The swim bladder of larvae at night was frequently so inflated that it constricted the gut (see fig. 8 in Uotani 1973). Larvae in the dark with filled swim bladders were motionless or slowly sinking. The body was oriented head down at an oblique angle to the water surface. After sinking a short distance, the larvae swam back to the water surface, a behavior closely resembling that of yolk-sac larvae (Hunter 1972).

TABLE 1.–Swim bladder volume (mm³) of preserved northern anchovy larvae from standard CalCOFI oblique plankton tows taken at night and in the day in southern California inshore waters.

Length class (mm)	Night samples N	Night samples Swim bladder vol (mean ± 2 SE)	Day samples N	Day samples Swim bladder vol (mean ± 2 SE)
11.0-11.9	23	0.044 ± 0.007	28	0.018 ± 0.008
12.0-12.9	20	0.073 ± 0.015	30	0.015 ± 0.004
13.0-13.9	24	0.124 ± 0.011	17	0.030 ± 0.016
14.0-14.9	14	0.128 ± 0.011	6	0.029 ± 0.003

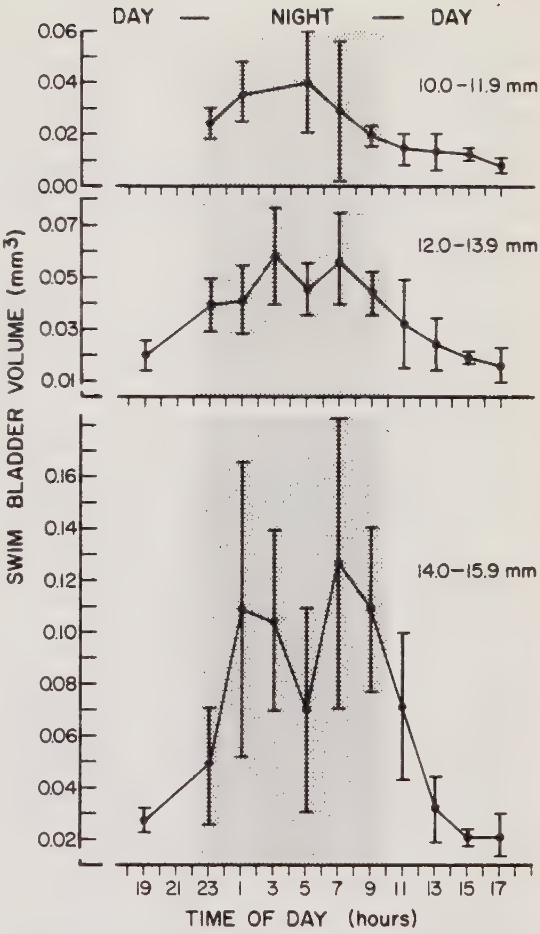

FIGURE 2.–Mean swim bladder volume ± 2 SE of mean for 2-h class intervals plotted at midpoint of each 2-h class. Data shown for three length classes of laboratory-reared northern anchovy larvae; the onset of dark was at 2200 h and onset of light at 1000 h. No transitional level of illumination existed between night and day.

Specimens with obviously inflated swim bladders occurred occasionally in day samples from the sea and laboratory but these were only a few percent of the larvae examined if the first 2 h after the onset of light are excluded. On the other hand, the occurrence of larvae with deflated bladders at night was more common. About 10% of the wild larvae and 20% of the laboratory-reared (12.0 to 12.9 mm) larvae had swim bladder volumes at night comparable to those in the day (Figure 3). The proportion of larvae with deflated bladders at night decreased with larval length.

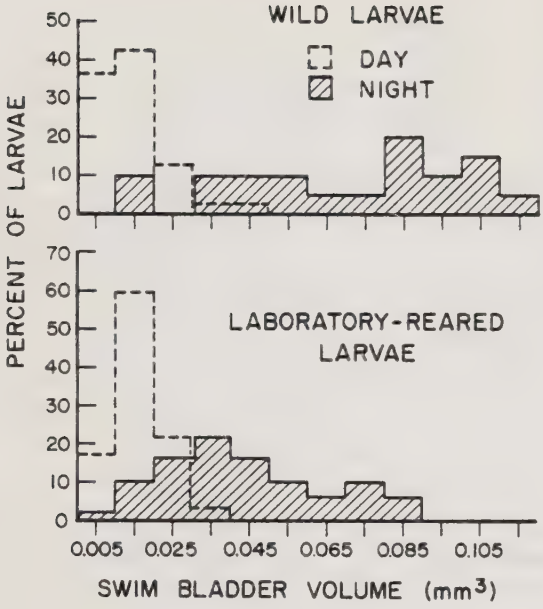

FIGURE 3.–Percent of northern anchovy larvae, 11.9 to 12.0 mm, at night (solid bars) and in day (dashed bars) having swim bladder volumes in various 0.01-mm³ classes; numbers on abscissa are midpoints of swim bladder volume classes. Upper panel, larvae from CalCOFI ichthyoplankton collections (preserved specimen length), $N = 20$ for night, and $N = 30$ for day. Lower panel, larvae reared in laboratory (live specimen length), $N = 49$ for night, and $N = 29$ for day. Data from 2-h after onset of dark and 2-h after onset of light were excluded in laboratory-reared larvae.

The mean swim bladder volume at night was greater for wild than for laboratory-reared larvae of the same length. The effect of preservation on larval length for larvae of this size is not known but a shrinkage of about 10% in length in the Formalin-preserved ichthyoplankton specimens would account for this difference. The effect of preservation on swim bladder volume is also unknown. In some of the preserved specimens, we noticed the bladder was filled with fluid but we did not routinely make an examination of the bladder contents.

Swim Bladder Inflation and Larval Length

The swim bladder was fully formed when larvae reached 8 to 9 mm but it usually was not inflated. To determine the larval size at which nightly inflation commenced, night and day samples from the laboratory were grouped into 1-mm length classes (9.0 to 9.9 mm, 10.0 to 10.9 mm, etc.), and the mean volume for day and night samples for each class calculated, and compared using the t test. The first 2 h after the onset of dark and the onset of light were excluded from the classes.

Some of the 9.0 to 9.9 mm larvae appeared to have inflated swim bladders at night but the night-day difference in swim bladder volume was not significant ($0.2 > P > 0.1$). Mean volumes for day and night samples were different in larvae 10.0 to 10.9 mm as were those for larvae in all succeeding length classes ($P < 0.001$). Thus, the threshold larval length for nightly inflation of the swim bladder occurred at about 10 mm, the point at which the means for day and night volumes diverge (Figure 4).[3] From this point, mean volume of night samples increased exponentially with length whereas that for day samples increased linearly.

Relation Between Sinking Speed, Swim Bladder Volume, and Larval Length

We observed that larvae with inflated bladders sank more slowly than those with uninflated

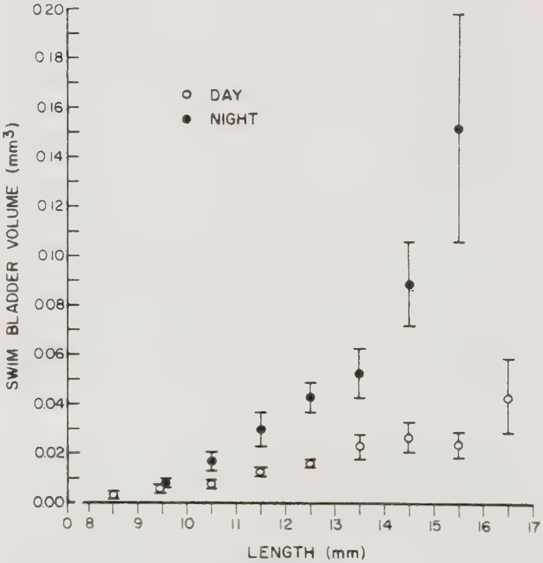

FIGURE 4.–Mean swim bladder volume ± 2 SE for laboratory-reared northern anchovy larvae for 1-mm classes of length plotted at the midpoint of each class. Solid circles are night (first 2-h after onset of dark omitted) and open circl [illegible] day (first 2-h after onset of light omitted).

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[3] Swim bladder inflation is reported to occur at 7 mm in *E. japonicus* (Uotani 1973). Comparison of his illustrations to those of Uchida et al. (1958) suggests Uotani's reported lengths are in error and that *E. japonicus* also inflates the bladder at about 10 mm.

bladders. At night, larvae were occasionally neutrally buoyant but most were slightly negatively buoyant.

To develop an equation for expressing sinking speed in terms of larval length and swim bladder volume, the data on sinking speeds were grouped into four classes of larval length: 10.0 to 11.9 mm, $N = 30$; 12.0 to 13.9 mm, $N = 41$; 14.0 to 15.9 mm, $N = 54$; and 16.0 to 17.9 mm, $N = 14$. A regression of sinking speed on swim bladder volume for each length class yielded the following slopes and standard errors for the regression lines: -3.040, SE = 2.339; -4.001, SE = 1.297; -4.8796, SE = 0.616; and -5.070, SE = 1.680, respectively. Covariance analysis of these data indicated that the slopes were not different whereas the intercepts for the regression lines were statistically different ($P = 0.01$). Since no difference existed in the slopes among the four groups, the common slope from the covariance analysis, -4.769, SE = 0.487, was used to express the relation between sinking rate and swim bladder volume for each length class (Figure 5, lower panel). When adjusted for the common slope, the sinking rate intercepts of the four regression lines showed a precise linear relationship when plotted against the midpoints of their respective length classes (Figure 5, upper panel). The equation for the intercept-length relationship was $y = 0.18L - 1.51$ where L is larval length (the midpoints of the larval length classes) and y is the intercept for the regression of sinking rate on swim bladder volume (the sinking rate at $V = 0$ in Figure 5). This equation was combined with the common slope to provide the equation given below:

$$S = 0.18L - 1.51 - 4.77V$$

where S = sinking speed in centimeters per second
L = larval length in millimeters
V = swim bladder volume (outside dimensions) in cubic millimeters.

We examined the changes in sinking speed of larvae from the time of hatching through the development of the swim bladder. These changes are of interest because they illustrate the timing of swim bladder development, its effect on buoyancy, and the advantage of a nightly inflation cycle. Data for sinking rates for larvae 4.0 to 9.9 mm were grouped into 1-mm classes and the means plotted at the midpoints of the class intervals except for the yolk-sac larvae (3.7 mm) which were all about the same length. For larvae 10.0 mm or larger, we calculated sinking speeds from the mean swim bladder volume given in Figure 4 using the equation given in the preceding paragraph.

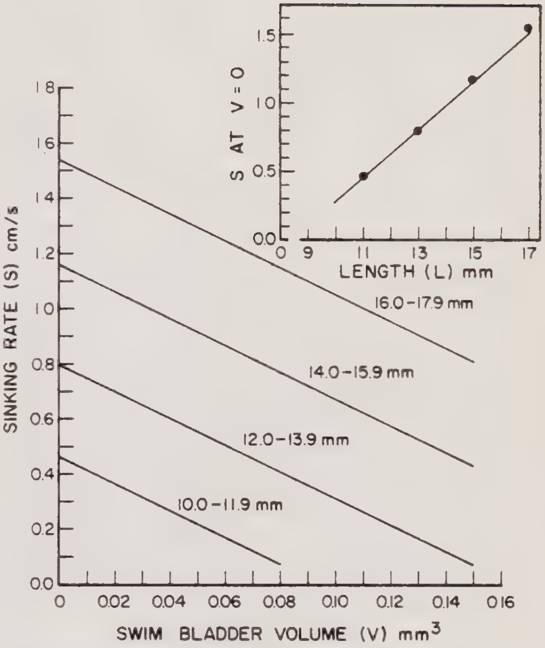

FIGURE 5.—The relation in larval northern anchovy between sinking speed (S), swim bladder volume (V), and larval length (L). Lower panel, regression lines show relation between sinking speed and swim bladder volume for the four classes of larval length indicated in the figure, when a common slope of -4.769 is used (see text). Upper panel, the regression of the y intercepts (S at $V = 0$) of the four regression lines on larval length (midpoints of the four length classes); equation for intercept line was $y = 0.18L - 1.51$. Final equation is $S = 0.18L - 1.51 - 4.77V$.

Sinking speed increased exponentially with length, when larvae sampled at night are excluded (Figure 6). The increase is roughly proportional to the cube of the length (curved line in Figure 6). This might be expected since sinking speed is dependent upon buoyancy which varies with the volume (L^3) and the difference in specific gravity between the fish and its medium. For estimating mean sinking speed for larvae with swim bladders in the day, or for those without swim bladders the equation $S = 0.094 + 0.000264L^3$ where L is length in millimeters and S is sinking speed in centimeters per second, gives a good fit to the data.

The length threshold for filling the swim bladder (about 10 mm) coincides with a rapid acceleration

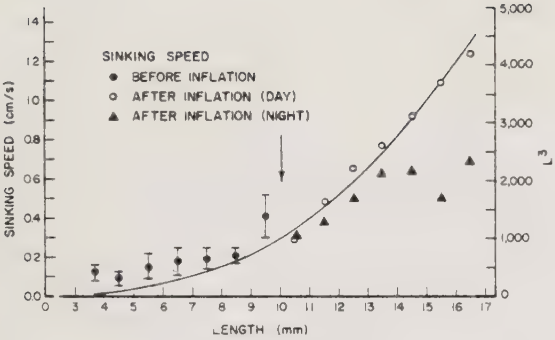

FIGURE 6.–Change in sinking speed from hatching through threshold of the initial inflation of swim bladder (arrow) of northern anchovy larvae. For larvae <10 mm, mean sinking speed ± 2 SE were plotted against the midpoint of 1-mm length classes, except for the first point which was for yolk-sac larvae and is plotted at average length for the class. For larvae >10 mm, sinking rates are estimated from the mean swim bladder volume given in Figure 3 using the general equation for sinking speed given in Figure 5. Open circles are estimates for the day and solid triangles for the night. Line is the cube of the length (L^3) plotted against length.

in the volume of the larva and its sinking speed. Thus, the timing of the swim bladder inflation may be related to these events.

The effect of night inflation of the swim bladder is also illustrated in Figure 6. For larvae 12 mm and larger, the average sinking speed at night appears to be relatively constant at about 0.6 ± 0.1 cm/s (22 m/h) while the sinking speed in the day increased exponentially with length. A larva 16.5 mm long had a sinking speed at night nearly half that of the day. Swimming speeds of larval anchovy while searching for food in the day, range from about 0.6 to 1.0 body length/s (Hunter in press). If a larva did not inflate the swim bladder at night, the swimming required just to maintain a position in the water would be equivalent to that used in the search for food in the day. Since larvae do not feed at night, filling the swim bladder would clearly be advantageous as an energy conserving mechanism.

Mechanism of Swim Bladder Inflation

It was not possible to determine if larvae in the tank sealed with mineral oil swam just below the layer of oil or into it because our view was from above rather than from the side. However, the mean swim bladder volume for larvae sampled at night in the sealed tank was less than that for larvae sampled on the previous night when the tank was not sealed (t test, $P = 0.001$, Table 2). The mean volumes of the swim bladders for larvae in the day and at night in the sealed tank were not different. This experiment suggests that anchovy larvae in the laboratory fill their swim bladders by swallowing air at the surface.

TABLE 2.–Mean swim bladder volume and mean length of northern anchovy larvae in sealed and unsealed containers.

Treatment	N	Mean length of larvae (mm ± 2 SE)	Mean swim bladder vol (mm³ ± 2 SE)
Unsealed tank:			
Night	12	13.9 ± 0.37	0.094 ± 0.037
Sealed tank:			
Night	18	14.1 ± 0.41	0.035 ± 0.008
Day	17	13.8 ± 0.86	0.026 ± 0.019

An analysis of the oxygen content of the swim bladder could suggest whether or not the gas in the swim bladder was secreted or taken from the air. Newly secreted gas would be expected to be oxygen (Wittenberg 1958), but if larvae were swallowing air the concentration should be about 21% oxygen. Our analysis did not agree with either pattern even though some measurements were made 30 min after the onset of dark. Samples averaged about 11% oxygen, consistently less than the atmospheric concentration (Table 3). Carbon dioxide levels (0.9 to 2.2%) were higher than atmospheric levels but little can be concluded because our experimental reading error was 1 to 2% owing to the small volumes used. It is probable that oxygen was lower than atmospheric concentration because it was absorbed from the bladder by the larva. Except for the first two observations in Table 3, oxygen concentration tended to decrease with time from the onset of dark. It should be noted that preferential removal of oxygen from swim bladder gases is not unique to anchovy larvae but is found in most fishes which have been studied (Wittenberg 1958).

The rate at which the swim bladder was filled also suggests that the filling is accomplished by gulping air. Larvae with filled swim bladders were captured 20 to 30 min after the onset of dark and the means were at a maximum by 2 h after dark. Uotani (1973) reported for *E. japonicus* that filling was completed by 1 h in the sea. Fishes that fill the swim bladder by secretion require much more time to fill the bladder, for example, *Stenotomus versicolor* (Mitchill) requires 10 to 12 h; *Anguilla rostrata* (LeSueur), 12 to 24 h; *Opsanus tau* (Linnaeus), *Prionotus carolinus* (Linnaeus), and *P. evolans* (Linnaeus), 24 h; and *Tautoga onitis*

TABLE 3.—Percent composition of swim bladder gas of laboratory-reared northern anchovy larvae sampled at night, listed in order of time of sampling.

Elapsed time after onset of darkness (h)	(min)	Number of larvae	Mean larval length (mm)	Composition of swim bladder gas (%) CO_2	O_2	N_2	Sample volume (μ l)	Oxygen in tank (ml/liter)
0	30	2	27.1	1.2	9.6	89.2	5.54	5.4
0	30	2	29.6	1.6	8.2	90.2	8.12	—
0	50	4	22.1	1.3	14.2	84.5	4.99	5.7
3	15	5	21.0	1.8	13.1	85.0	6.08	5.0
4	20	3	25.3	2.2	11.1	86.7	7.18	5.1
6	25	8	19.3	0.9	12.7	86.4	4.85	4.6
6	25	7	18.9	0.6	12.6	86.9	4.05	5.0
7	35	6	22.1	1.4	9.1	89.5	6.06	4.9
8	10	6	20.1	0.6	9.5	89.9	3.70	4.8

Linnaeus, about 24 h (Wittenberg 1958). Considering the evidence presented here, and the apparent lack of gas secretion in clupeoid fishes in general (Brawn 1962), the most tenable hypothesis is that swim bladder inflation is accomplished in larval anchovy by taking in air at the water surface.

Vertical Migration

If anchovy larvae fill their swim bladders each night by swallowing air, they must either remain near the surface throughout the day and night or migrate to the surface at dusk.

We reexamined the original data collected by Ahlstrom (1959) to determine if any evidence existed for vertical movements in northern anchovy larvae. Ahlstrom (1959) made extensive horizontal tows for fish larvae with opening and closing nets and presented the average number of larvae of all lengths at various depths. We separated his original length data into two length classes: larvae <11.75 mm (preserved standard length) and larvae ≥11.75 mm for night and day collections; we omitted those collections occurring near dawn and dusk. Unfortunately, only 14 larvae ≥11.75 mm were taken in the day while 279 were taken at night but the depth pattern in the day collections was relatively consistent. Larvae <11.75 mm were more abundant: $N = 6{,}456$, night; and $N = 331$, day.

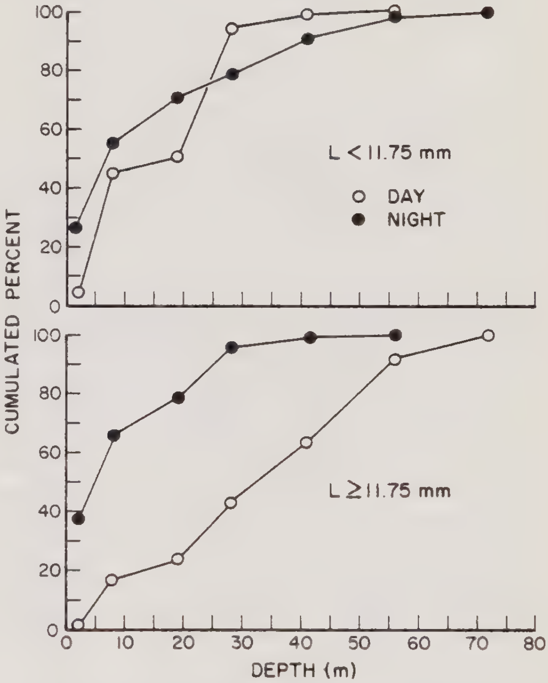

FIGURE 7.—The vertical distribution in the sea of northern larvae at night and in the day for two length classes; length <11.5 mm, upper panel, and length ≥11.5 mm, lower panel (lengths for preserved specimens). Numbers of larvae taken at each depth were cumulated starting at the shallowest tow (5 m) and expressed as the cumulated percent of the total larvae taken. Data are from Ahlstrom (1959).

At night, over 50% of the larvae ≥11.75 mm were taken in the upper 10 m whereas in the day the upper 10 m contained less than 10% of the larger larvae (Figure 7). About 50% of the larvae <11.75 mm occurred in the upper 10 m, but no obvious difference between day and night samples existed. These results are in general agreement with those of Ida (1972) who studied the vertical distribution of the Japanese anchovy, *E. japonicus*, a closely related species that also has a diel rhythm in swim bladder inflation (Uotani 1973). Ida (1972) found a striking diel change in the vertical distribution of *E. japonicus* with the maximum numbers occurring at the surface at night and at 20 to 30 m during the day with the movement to the surface occurring at twilight. Examination of the size frequency histograms from some of the collections led Ida to conclude that the diurnal change was caused by the vertical migration of the larger larvae (10 to 15 mm).

The diel vertical movements that appear in larval anchovy at the time of swim bladder inflation probably persist into adult life. The adults, however, are quite variable in their behavior which changes with size of school and season (Mais 1974). Vertical migration is most noticeable in large schools which are deep during the day (119 to 220 m) and rise to the surface and disappear as sonar targets at dusk. These schools reform and descend at first light in the morning (Mais 1974).

Possible Adaptive Advantages

Inflation of the swim bladder reduces the energy required for maintaining a position in the water column. This reduction in sinking speed could represent an important energy savings for larval anchovy because they do not feed at night and swimming can not be used in the search for food. The major energy cost of a diel rhythm of swim bladder inflation is the required vertical migration to the surface. Laboratory work suggests that anchovy larvae, by modification of swimming speed and direction of turning, are able to find and remain in area of high food density (Hunter and Thomas 1974). Thus, it is possible that a larva could follow an upward and downward movement of food at dusk and dawn. In this case the added cost for vertical movements would be slight since the energy spent in swimming could be used in searching for food. It is unlikely, however, that this condition could always be met. Thus, the energy saved at night by inflation of the swim bladder should exceed that used in vertical migration. Assuming the energy used per centimeter swum is the same for vertical migration as for maintaining a position in the water at night, the energy used in a round trip vertical migration of 100 m would be equivalent to that used to maintain a position for 10 h at night when the sinking speed was 0.28 cm/s. Thus, the difference between day and night sinking speeds would have to exceed 0.28 cm/s before a 100-m round trip could be considered an energy sparing mechanism. The difference in sinking rates exceeds 0.28 cm/s for larvae 13.5 mm and larger (Figure 6). This difference increases with larval length suggesting that the vertical range of migration over which energy savings are possible increases with length. In addition, the difference between day and night sinking speeds may be underestimated because sinking speeds were measured at the surface. If larvae descend during the day the gases in the swim bladder would be compressed, increasing body density and thereby increasing the sinking speed for larvae in the day.

These calculations are, of course, a great oversimplification, but they do illustrate that the energy saved by inflation of the swim bladder at night could exceed the cost of a vertical migration and that the possible range of migration could be greater for larger larvae.

The energy costs of maintaining a position in the water column for fish with and without swim bladders have been calculated by Alexander (1972). His calculations are not appropriate for anchovy larvae at night because he considered fish without a bladder to be continuously swimming and gaining lift from the pectoral fins. The behavior of an anchovy at night that failed to inflate the swim bladder would probably resemble one with an inflated bladder. It would sink motionless at an oblique angle to the water surface and interrupt sinking by bursts of near vertical swimming. To maintain a position, these bursts of swimming would have to be of longer duration or of greater frequency than if the swim bladder were filled.

In addition to an energy sparing mechanism, a nightly pattern of swim bladder inflation could possibly reduce predation. Some predators of larval fishes, for example chaetognaths and medusae, use the movement or turbulence produced by prey for detection and attack (Horridge 1966; Newbury 1972). Thus, the reduction of activity produced by slower sinking speeds could reduce predation. The vertical migration of the larvae could also result in exposure to different and possibly less hazardous predators at night. It would also serve to aggregate larvae, thus facilitating social contacts necessary for the development of schooling which begins at about 15 mm.

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THE CALIFORNIA SQUID FISHERY

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1. INTRODUCTION

Numerous species of squid are found in the California Current system, but only the common market squid, *Loligo opalescens* (Berry, 1911) is the object of a fishery. A few tons of the jumbo squid, *Dosidicus gigas* (d'Orbigny, 1835) have been landed from time to time but never in sufficient quantity to support a sustained fishery (Croker, 1936). Most other species are either too small or not readily available to the fisheries. It should be noted, however, that exploratory fishing efforts have never been directed by U.S. fisheries toward locating and attempting to fish squid on the high seas off the west coast. An exploratory cruise conducted by a Japanese vessel in 1971 failed to catch substantial quantities of squid between British Columbia and California; however, the vessel made good catches (probably *D. gigas*) off the southern tip of Baja California, Mexico (Anon., 1971). This report deals only with the fishery for *Loligo opalescens* in California.

Loligo opalescens (Fig. 1) is a small squid. In commercial landings at Monterey, California, males averaged 150 mm in mantle length and weighed 70 g, while females were 140 mm and 50 g (Fields, 1965). Maximum mantle length was about 190 mm for males and 180 mm for females (*Ibid.*). Nearly all squid taken by the commercial fishery are mature and are caught during the spawning season.

2. LIFE HISTORY

2.1 Reproduction

Adults of *L. opalescens* congregate in vast numbers in shallow waters to spawn. McGowan (1954) directly observed spawning on sandy bottom with rocky outcroppings, primarily at depths of 15 m and down to at least 35 m. The egg capsules were laid in clusters, the largest of which was about 12 m in diameter. Most clusters are considerably smaller, however. Only a few animals are known to feed on egg capsules of *L. opalescens*. *Patiria* (MacGinitie and MacGinitie, 1949) and possibly other starfish may feed on the eggs, and the junior author has observed large numbers of white sea urchin *Lytechinus* sp. aggregated around and over clusters of squid eggs. In an aquarium each of several females deposited overnight an average of 20 capsules, each containing 180 to 300 eggs (Fields, 1965). Larval squid hatch at 2.5 mm mantle length after 3 to 4 weeks at 16°C (Fields, 1965) and 4 to 5 weeks at 13.6°C (McGowan, 1954). Mass mortality occurs after spawning, as evidenced by large numbers of dead squid (Fig. 2) on the bottom in spawning areas (McGowan, 1954). Whether or not all squid die after a single spawning season is not known.

2.2 Growth and Longevity

Loligo opalescens has been reared from eggs in a laboratory tank for periods up to 100 days (Ann Hurley, National Marine Fisheries Service, La Jolla, pers. comm.). Growth rate was slow for the rearing period, averaging about 2.5 mm/month mantle length. Whether this growth rate truly reflects natural growth in the wild remains to be seen, but it seems rather low. Fields (1965) estimated longevity of about three years, with a growth rate of 4 mm/month using monthly modal progression of the length-frequency distribution, but his conclusion was based primarily on spawning animals caught by the Monterey commercial fishery. Such squid would presumably be expending more energy on reproductive processes than body growth. Field's data on juveniles showed a similar growth rate, but his modal progressions followed squid spawned in different years, and caught at several localities by different methods.

Recent evidence suggests that squid may exhibit daily growth increments in the statolith (Brothers et al., in press). The number of growth increments in the form of fine lines or lamallae showed good correspondence to actual age of squid reared in the laboratory (Edward Brothers, Inter-American Tropical Tuna Commission, La Jolla, California, pers. comm.). In wild squid ranging in size from 110 to 160 mm mantle length, the number of lamallae numbered 320 to 450. If the lamallae truly represent daily growth increments, they suggest a longevity of about one to one and a half years (Jerome Spratt, California Dept. of Fish and Game, Monterey, California, pers. comm.).

2.3 Distribution and Migration

Adults of L. opalescens are found from British Columbia (Fields, 1965) to central Baja California, Mexico. Spawning concentrations or egg masses have been occasionally reported from British Columbia, Puget Sound, and Punta Eugenia (Lat. 27°51'N), Baja California (Okutani and McGowan, 1969), but the main spawning grounds are apparently at Monterey and at the Channel Islands off southern California. Large spawning aggregations are also known to occur in many areas along the mainland coast from San Diego to Monterey, California (Ally, Evans and Thompson, 1975). The months of heaviest concentration at the Channel Islands are December to March, and off Monterey, May to July. A minor peak in availability of spawning squid, reflected in catch statistics, used to occur regularly in November at Monterey (Fields, 1950), but recently this peak has not been evident consistently.

Larval distribution of squid has been examined in detail by Okutani and McGowan (1969). They found larvae of L. opalescens in nearshore waters from the southern tip of Baja California to San Francisco, with greatest numbers occurring between Pt. Conception and southern Baja California in winter and spring. However, considering the heavy annual concentration of spawning activity at Monterey in spring and summer, one would expect to find correspondingly high concentrations of larvae during this period off central California. Perhaps sampling patterns or some other factors led to underestimation of relative abundance north of Pt. Conception.

Information on distribution of juvenile stages is scanty. Juvenile L. opalescens are found in many inshore localities along the central and southern California coast, but large concentrations are rarely encountered. This may simply be due to lack of sampling effort and inadequacy of fishing and sampling gear for catching juvenile squid.

Depth distribution of L. opalescens has not been investigated extensively. Although it is clear that the greatest concentrations of spawning squid occur in shallow water, egg masses and adult squid have also been taken by bottom trawl in depths of 180 m. Squid of various sizes from juveniles to adults have been observed near the surface at Monterey feeding on aggregations of euphausids, and in turn being consumed by birds (G.V. Morejohn, Moss Landing, California, pers. comm.).

Movements and migratory patterns of L. opalescens are unknown. Okutani and McGowan (1969) found a progressive northward movement in number and frequency of occurrence of larvae, starting in winter from southern Baja California. This does not necessarily mean that adults or subadults migrate in similar fashion. Widespread spawning, both in time and geography, makes it difficult to interpret observed distributional patterns, particularly because adults presumably die after spawning. Further, lack of knowledge about homing behaviour and population structure hampers our ability to gain an insight into migratory patterns.

2.4 Sex Ratio

Fields (1965) concluded from extensive sampling through several years of commercial landings at Monterey that the sex ratio of L. opalescens was essentially 1:1. Large imbalances in sex ratio, with either males or females predominating, often occurred with particular schools of squid, however. His samples were primarily taken from squid fishing vessels, but he also examined squid caught incidentally in other fisheries. Unfortunately, Fields lumps several years of data and does not give sex ratios by seasons or smaller entities. Ronald Evans (Moss Landing Marine Laboratories, Moss Landing, California, pers. comm.), found males predominating with 56 percent of the total in the 1974 Monterey catch. In the 1974 southern California catch, he found 59 percent males. Samples from the two areas may not be comparable because of different fishing methods. Light-attraction methods used in southern California may be selective for males (J.R.R. Ally, California Department of Fish and Game, Long Beach, California, pers. comm.). Interestingly, McGowan (1954) found 63 percent males when he sampled dead and dying squid during a period of spawning activity.

2.5 Feeding Relationships

Fields (1965) found differential feeding patterns in spawning and nonspawning schools of squid. Female squid sampled from the commercial catch at Monterey nearly always had empty stomachs, while 37 percent of males had some food. The bulk of this food consisted of squid, presumably L. opalescens. Stomach samples taken from nonspawning squid caught incidentally with fish in roundhaul nets revealed entirely different patterns. Both males and females had food in the stomachs, and crustaceans (euphausid and mysid shrimp) and fish were predominant. Anatole Loukashkin (California Academy of Sciences, San Francisco, California, pers. comm.) found about equal amounts of fish and crustacean remains in the stomachs of squid caught by jigging. Stomachs from spawning schools were usually empty.

Loligo opalescens is undoubtedly a major food item for the whole spectrum of carnivores occurring in the California Current system. Predators include birds, sharks, bony fishes, and marine mammals.

2.6 Populations and Abundance

Studies on population structure of Loligo opalescens have only recently been initiated. A recent study disclosed statistically significant differences in some morphological characteristics between squid from southern and central California (Ronald Evans, Moss Landing Marine Laboratories, Moss Landing, California, pers. comm.). Southern California squid were longer, had thicker mantles, and had longer and wider fins. Curiously, the Monterey squid weighed slightly more than southern California squid. Another study, involving electrophoretic techniques on enzyme and blood protein distribution, suggests the existence of more than one population of squid (Jay Christofferson, California State College, Stanislaus, California, pers. comm.).

No good estimate of the abundance of L. opalescens is available at present. Various estimates of the potential annual yield have been given, ranging from over 100 000 tons (Voss, 1973) to 300 000 tons (Gulland, 1971). The latter figure seems high, but may include other squids found in the California Current system. The highest annual catch, 19 012 tons, was taken in 1946.

3. THE FISHERY

The squid fishery in California is essentially two fisheries, one centred at Monterey and the other in southern California at the Channel Islands (Fig. 3). Fishing methods, price, and seasons are different in the two areas.

Earliest accounts of the Monterey squid fishery go back to the late eighteen hundreds, when immigrant Chinese fishermen harvested squid at Monterey Bay (Collins, 1892). Squid were attracted to a lighted torch hung from a small skiff. When sufficient numbers had accumulated two vessels surrounded them with a purse seine 55 m long and 5.5 m deep (Ibid.). In 1905 immigrant Italian fishermen introduced the lampara net at Monterey, and this gear has predominated there to the present time.

The fishery started somewhat later in southern California, beginning in earnest in 1953 when over 2 450 tons were harvested. Previous to that year the high catch was under 350 tons.

Historical catch data (Fig. 4) show the Monterey fishery (which includes landings at Moss Landing, located about 30 km north of Monterey) predominating until the early sixties, when the southern California catch started to increase. In recent years the southern catch has even exceeded the Monterey catch (e.g., 1965, 1970, 1973, 1974). The ex-vessel price (Fig. 5) has always remained higher at Monterey, however. A considerable price differential exists between prices paid by freezers and by canners of squid, with the former paying 1.5 to 4 times more than the latter. Monterey processors have always paid more than southern California processors, both for freezer and canning squid. Reasons for this are vague but apparently are related to quality of squid, union activity, and market conditions.

Usually, squid are sold to freezer plants because of the higher price, and canners receive the excess beyond processing capacity of the freezer plants. Thus, in times of high availability, more squid is canned, and the average value of squid is consequently lower. The freezer plants usually apportion the amount they can handle to several vessels. A few vessels in southern California fish exclusively for canners, electing to fish for a lower price to be assured of a larger market.

The bulk of the California squid catch is canned or frozen and exported to Europe. Lesser amounts are exported to Latin American countries and to the Orient, particularly the Philippine islands. Domestic consumption is mostly in frozen form, and a considerable amount of frozen squid is also used as bait in both commercial and recreational fisheries.

Several fishing methods are employed to capture squid in the California fishery. The methods are dictated by fishing regulations, economics, behaviour of the squid, and fortuitous encounters by fishing vessels that are searching for other species.

The fishing seasons in the two areas are different, with landings peaking in winter in southern California and early summer in Monterey (Fig. 6). A secondary peak used to occur in Monterey in November (Fields, 1965), but this peak has been small in the average catch for the last 20 years. In southern California, fishing generally starts in December at the lower Channel Islands of Santa Catalina and San Clemente Islands. Nearly all squid landed are caught by light-attraction methods, but some are also caught by purse seine. As the season progresses, the squid appear to move northward, and catches from Santa Cruz Island and off Port Hueneme increase. Purse-seining activity also increases, particularly after the closure of the anchovy (Engraulis mordax) reduction season in the middle of May.

3.1 The Southern California Fishery

Squid is usually located with the aid of depth sounders. Both flasher type and paper recorder sounders are used, and many makes and models are represented in the fishery. Frequencies of the depth sounders vary from 38 to 125 kHz. At present there appears to [illegible] no preference for any single type or frequency of echo sounder, but most are relatively inexpensive sets that operate at 50 kHz. At least two vessels employ sonar to good advantage.

The model used by both, Wesmar SS-150[1], operates at a frequency of 160 kHz and is reported to be quite effective in locating schools of squid. However, positive identification as to species is not usually made from echo sounder marks alone. In order to confirm identification, fishermen often employ bare treble hooks to snag animals located by echo sounders. Some fishermen appear to be able to distinguish squid from fish (usually anchovy or jack mackerel) by the general form of the school as revealed by the depth sounder, and through the school's behaviour under attracting lamps.

At night bioluminescence also aids in the detection of squid schools. Another indication of squid is the presence of predators - pilot whales (Globicephala macrorhynca), sea birds, and occasionally, sea lions (Zalophus californianus).

Scouting usually commences before dark and continues into the night until squid are found. Most searching is concentrated near shore in depths of 20 to 70 m. No searching is done in deeper waters where squid are undoubtedly present, because fishing operations are limited to depths in which the vessels can anchor. Further, when squid are too deep they will not respond to the attraction system employed by the southern California fishery. Most fishing is done over depths of 24 to 33 m (J.R.R. Ally, California Department of Fish and Game, Long Beach, California, pers. comm.).

Once a promising school is found, the vessel is anchored in the area of heaviest concentration (except when purse seining, which will be discussed later). At dark, attracting lamps are turned on. The lamps consist of two or more 1 500 Watt incandescent lamps placed high above on the mast (Fig. 7). Other types of lamps, such as quartz-halogen and mercury vapour, have occasionally been used, but most fishermen prefer the incandescent lamp. Concentrating lamps, usually of similar intensity, are situated about two metres above the water. These lamps are also turned on at the same time. After a period of time, which depends on the behaviour of the school, the squid come to the surface. School size varies from a few tons to over 100 tons (Fig. 8). The squid swim in a circle, usually heading aft outboard, turning at the edge of the lighted area, and passing alongside the ship on both sides directly under the concentrating lamps. Squid normally swim with a heading into the current toward the lamp. Thus, when current and wind directions are markedly different, the vessel is placed under power to maintain the bow headed into the current. A power-assisted brail is the principal fishing gear used in southern California (Fig. 9). The hoop of a typical brail is about 1.1 to 1.5 m in diameter, and the netting, constructed of 2.5 cm stretched mesh, is about 150 to 200 meshes deep. Small purse rings are sewn in at the bottom of the net to facilitate quick opening and closing of the brail. During operation, one man guides the brail into the water holding a handle 3 m long. The same man holds on to the chain purse line. The brail is lowered and raised by a second man with a hydraulic or mechanical winch. As the brail is manoeuvred into the water ahead of the swimming squid, a third man pulls the brail toward the stern of the vessel, through the concentration of squid. At the end of a sweep, the winch man lifts the brail out of the water and lets the net rest on the gunwhale or deck for several seconds to drain most of the water (Fig. 10). The brail is again raised until it is poised over the fish hold, and the bottom is opened. The brails hold about 250 to 500 kg of squid. A variation called the "Canadian" or "sock" brail is sometimes used. This brail has a net depth of about 6 m and does not have purse rings. During operation, the brail is passed several times through the school of squid. To bring the catch aboard, the hoop is placed on the opening of the fish hold, and the end of the brail is lifted upward by means of a line passing through a block on the mast. Although most vessels carry three crew members, two-person operations are not uncommon, and in one case a single man uses a power-assisted brail effectively, although the amount he can catch is limited.

Squid are usually oblivious to brailing activity; thus operations often continue until the hold or the market order is filled. Occasionally commotion at the surface will cause squid to dive, halting fishing operations. Active predators such as dogfish sharks (Squalus

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1/ Mention of commercial products by name does not constitute or imply endorsement by the National Marine Fisheries Service or California Department of Fish and Game acanthias), pilot whales, sea lions, and diving birds can cause the squid to sound, while slow-moving blue sharks (Prionace glauca) cause little alarm to the school except when large numbers of sharks are present. Thus, fishermen are obliged to continuously chase predators away from the immediate area.

When a school of squid behaves erratically, it becomes impossible to use a large brail, because the disturbance causes the squid to sound. In such cases, fishermen often resort to the use of hand-operated brails, gently dipping a few kilogrammes per scoop.

In the southern California fishery the primary fishing method is the power-assisted brail, used in conjunction with attracting lamps. A unique method of catching squid with a hydraulic centrifugal pump and the traditional light attraction system was developed by one of the authors and a commercial fisherman (Kato, 1970). The pump, a Marco Model U-230 Capsulpump (Fig. 11) was designed to handle fish, but we found it also useful for catching squid. At a total static head of 5.2 m and hydraulic fluid flow of 75.7 l/min (under a pressure of 84 kg/cm^2 or 1 200 psi), the pump will discharge about 400 tons of water per hour through a discharge hose with a diameter of 203 mm. A 20 Hp electric motor supplies sufficient power for the hydraulic system.

After many trials an effective system was developed which utilized a floating wooden funnel (Fig. 12). The funnel measured about 2 m wide, 1.5 m high, and 2 m long. A small 500 Watt quartz-halogen underwater lamp was placed at the interior end of the funnel where two vertical bars were also installed to prevent sharks from being sucked into the pump. Floats were used to keep the funnel at the surface. A small boom was sufficient to handle the gear which weighed about 200 kg. A rubber fish hose led from the pump to the gunwhale, where a steel elbow was used to prevent kinking. Another section of rubber hose led from the elbow to a steel separator, which removed water over the side. The separator was lined with galvanized cloth, 9.5 mm square mesh.

Through continued experimentation the commercial fisherman, Madison Dee May, improved the system to correct some flaws. He found that the lower wing of the funnel could be constructed of 50 mm (stretched mesh) netting and the upper wing left open, without lowering the catch rate (Fig. 13). This funnel measured about 1.25 m square at the opening, tapering to 0.32 m square at the pump. The length was about 1.20 m. This innovation aided in preventing the funnel from moving back and forth violently when wave action was high and reportedly was effective in winds up to 25 knots (Madison May, San Pedro, California, pers. comm.). Further, the open top wing eliminated the need for an underwater lamp within the funnel. It should be noted that squid actually swim into the funnel, and strong suction is not necessary for the pump system to be effective. Indeed, when squid lie almost motionless at the surface, as sometimes they are wont to do, the squid pump is quite ineffective. May also suspected that water splashing over the side of the vessel from the separator scared some schools of squid. The black, foamy water apparently disturbed the squid or blocked out the light. To resolve this problem, he designed and built a separator which was completely enclosed. Two hoses leading from holes fed by a trough carried the water from the separator to a depth of 2 m under the surface. Surface foam was thus largely eliminated. To facilitate handling and eliminate need for a connecting elbow, the pump was turned 90° from its normal vertical position and the intake attached directly to the funnel.

To date only one fisherman has successfully used the pump system. One other vessel was equipped with a pumping system, but for various reasons it was not successful in catching squid. Others have indicated their intention of installing a pump, but none has done so yet.

Probably the greatest advantage of the squid pump over the brailing method is the possibility of reducing the crew size, and the dramatic reduction of physical labour. The pump can fish for sustained periods without rest, unlike crew members. When squid are active, the pump can easily outfish the brail. However, when squid lie nearly motionless at the surface, brailing is faster. At times when squid concentration is low, the pump can fish continuously, resulting in a substantial catch after several hours, while brailers usually will not attempt to fish until a good concentration of squid has accumulated. A major disadvantage of the pump is that two to five percent (depending on the pumping speed) of the heads of squid are torn loose.

It is difficult to compare the effectiveness of the two methods of fishing, because we lack information concerning important variables such as vessel capacity, market limits, fishing effort, and skill of individual fishermen. During the 1973/74 season the fishing vessel, PACIFIC TROJAN, which used a fish pump as well as the brailing method, caught 719 tons of squid in 43 delivery days (i.e., days when catches were landed) for an average of 16.7 tons per day. The range in catch per night varied from under a ton to 54 tons. PACIFIC TROJAN'S catch amounted to 14 percent of the total catch taken during that period by 20 to 25 vessels. Thus, other factors aside, pumping was relatively efficient. Generally, squid were pumped aboard for relatively short periods, with catches commonly reaching 15 tons per hour. This amount was sometimes brought aboard in ten minutes. Catches of 75 to 85 tons have been made with the pump in one night's fishing by PACIFIC TROJAN in previous years.

Cost of the pump, including hydraulic hoses and fish hoses, is presently about U.S.$ 5 000. Construction of a separator, chutes, and a funnel costs around U.S.$ 1 000.

Southern California has yet another method for catching squid, i.e., purse seining. No special seines are used for catching squid, but the anchovy and jack mackerel seines are also used for catching squid when the opportunity arises. Typically, the seines are 460 to 550 m long and 64 to 73 m deep. The anchovy net has a stretched mesh of 17 mm and the mackerel net of 35 mm (Anthony Pisano, Manager, Fishermen's Cooperative Association of San Pedro, pers. comm.). Like brail fishermen, purse seiners use bioluminescence, predators, and depth sounders to locate squid. Most of the vessels are equipped with sonar which adds a further dimension to their searching capabilities. Most fishing is done at night although day fishing is not rare. Fishing operations follow the same procedure used in most single boat purse seining operations. Sometimes squid are attracted to the surface with lights from the vessel. Then a skiff bearing a small portable lamp is used to hold the squid while the vessel extinguishes other lights and makes a set around the skiff. This method is not preferred because of the large number of predators, particularly sharks, attracted to the scene. When these animals are caught in the seine it is difficult to transfer the catch into the hold, a task often accomplished with a 300 mm Marco Capsulpump. Further, sharks outside the net often bite and tear the bag of the net during the transferring operation. During most years low market demand and small shoreside handling and processing capacity discourage the use of purse seines, which are capable of catching large quantities of squid. Late in the fishing season, from April through July, landings by seiners increase, while landings by brailers decrease. It is not clear why this situation occurs. One factor is reduced fishing effort by brailers because of the beginning of the albacore (Thunnus alalunga) season in summer. Most squid brailers turn to albacore as soon as this tuna, which is the principal source of their income, appearsoff the west coast. Further, as squid move progressively northward late in the season, the market and landing facilities become too distant for most of the brail fleet, which is comprised of smaller vessels. Because of the length of time it takes to make a round trip from the fishing grounds to port, fishing can be conducted only on alternate nights, and since these vessels can only carry 15 to 30 tons of squid, the fishery is uneconomical. It is also held that squid are not strongly phototropic during the summer months. On the other hand, purse seiners find anchovy fishing declining in late spring, and after mid-May, the season is closed. Thus they turn to other fisheries, including squid.

A unique method is sometimes used by one vessel for capturing squid and maintaining them alive for bait. Hatches have been cut into the sides of the vessel below the waterline. Each hatch leads to a divided compartment. When squid are crowded alongside the vessel underneath a concentrating lamp, the hatch is opened, causing the squid to be sucked into the vessel's hold together with the rushingwater. The light is then moved in front of another hatch and the procedure repeated. Squid caught and kept in these hatches remain viable for several days, and are sold primarily to recreational fishermen for bait.

Squid fishing vessels in southern California are of many varieties. Except for the purse seiners, all are combination vessels, used primarily in trolling or pole and line fishing for albacore tuna during summer and autumn. These vessels range in overall length from 10 to 28 m, with gross tonnages of 15 to 100 tons. Most vessels are equipped with hydraulic power and electric (AC) generators. Although nearly all vessels are equipped with refrigeration, usually a spray-brine system, squid are not refrigerated. Catches are hauled to fish plants immediately after fishing is terminated each night. About 15 vessels (excluding purse seiners) participate in the fishery regularly, while a few others engage in the squid fishery occasionally.

During unloading, the fish hold is flooded with water, and a small brail is used to transfer fish from the hold into metal tubs containing slush ice. In some cases pumps and moving belts are used to unload squid directly to a cannery or into transport trucks.

3.2 Monterey Fishery

The squid fishing method in Monterey Bay is determined primarily by California State fishing regulations. Purse seining was outlawed in 1953 because of possible effects on squid eggs. Spawning squid occur in shallow waters in the fishing grounds in Monterey Bay, and the lead line of purse seines drags across the ocean floor, uprooting the sessile egg masses. Another law which limits fishing methods, introduced in 1959, is the ban on the use of lights to attract squid. Thus brailing and pumping methods are effectively excluded. Reasons given for the passage of this law are many and varied, and there seems little chance of repealing or modifying it in the near future, despite recommendations to that effect by the California Department of Fish and Game. One reason given is that fishermen felt they needed protection from plant operators who in the past were able to catch substantial quantities of squid without vessels by employing lights and dip nets at their piers and floating unloading platforms. Fishermen also felt that bright lights disrupted spawning activity, and processors thought that light-attracted squid were lower in quality.

Squid at Monterey are caught with a roundhaul net called a lampara. Specifications for large and small lamparas are given by Scofield (1951) who defines a lampara as a roundhaul net with "...a large central bunt and relatively short wings of larger mesh. The two wings are pulled simultaneously." Lampara nets have been used to catch squid in Monterey Bay since 1905 when it replaced the purse seine that had been used by Chinese fishermen since at least 1863 (Fields, 1950). Some purse seines were used during the late forties but were outlawed in 1953. The bunt of the present-day lamparas has a mesh size of 32 mm (stretched). The corkline is usually 55 to 73 m long over the bunt. The leadline is usually less than 36 m long (sometimes as short as 12 m) below the bunt. The corkline of each wing is 145 to 190 m long. The leadline is usually 10 percent shorter so that it precedes the corkline as the net is hauled (Fig. 14), minimizing chances of squid escaping downward. Adjacent to the bunt the mesh size in the wings is 100 mm stretched and increases toward the wingtips to 150 to 230 mm. The wings of some nets taper to a point; others are cut nearly square. They are usually about 55 m deep where they join the bunt. The entire net is usually made of netting twine R 610 tex or R 700 tex (American number 8 or 9), but lighter netting yarns are sometimes used in portions of the wings. Further details on construction of lampara nets are given by Higgens and Holmes (1921), Scofield (1951), and FAO (1972).

Fishermen began replacing and repairing their cotton nets with Marlon (mixed polymeric) in the early fifties. In spite of its greater bulk, this Japanese synthetic netting material was favoured over nylon (polyamide) because of its softness, superior knot-holding qualities, and lower cost. Presently fishermen use nylon because its price has come down.

Most depth sounders used to locate squid in the Monterey area are of the flasher type. Frequencies are similar to those used in southern California. At least one fisherman tried to use sonar, but the wakes created by ten to 20 boats scouting an area of less than one square mile created so much interference that he was unable to locate squid. Squid are commonly located by searching for bioluminescense created by plankton when disturbed by schools of moving animals. The top of a school of squid tends to remain deeper than that of many other species located by luminescense, and the luminescense is more diffused by the thicker layer of water between the squid and the fisherman's eye. Spawning schools of squid also tend to swim in one direction, unlike some fishes.

As in southern California, the presence of predators indicates presence of squid. Predators used to locate squid schools at Monterey include marine birds, California sea lions (Zalophus californianus), and since about 1970, sea otters (Enhydra lutris).

In most years extensive scouting is normally not required during the height of the season. The fleet simply proceeds to the end of the breakwater of the Monterey boat harbour, and vessels manoeuvre for positions within the few hundred square metres in which squid are densest. There is much exchanging of oaths, and the question of where to set the net is often decided on the basis of where the safety of the crew, vessel and net is most secure. When species composition of schools is questionable, it is common practice to allow the first vessel to complete a set before the other vessels begin theirs. Vessels usually leave port around midnight except in periods of low availability when vessels embark shortly after dusk. Scouting is conducted outside the edge of an existing kelp bed which is in 20 m of water. Greatest depth scouted is around 60 m. The lampara nets generally fish to a depth of 35 to 55 m.

When a school of squid has been located, a small skiff, carrying the end of one towline attached to a wing, is released from the stern of the vessel. The remainder of the net, along with a length of towline, is pulled over the stern as the vessel makes a counterclockwise encircling manoeuvre, returning to the skiff. Sections of the bunt are usually manually thrown overboard to allow it to sink deeper. In a few cases, a skiff is not used; in its place a large lighted buoy with the end of one towline tied on is used. After the towline is retrieved from the skiff or float, both ends of the net are hauled simultaneously with the aid of powered net haulers or gurdies (Figs. 15 and 16). Most gurdies are made from automobile differentials and the net rollers constructed of automobile tires. Although a few gurdies are powered mechanically by the main engine, most are powered hydraulically. The lead lines close as the wings are drawn together, and the squid are thus trapped. While the wings are being hauled, a submerged flashing light is often hung from the vessel to deter squid from escaping between the wings. Loud hammering on the deck or gunwhale also serves the same purpose. The boom is used to bring in the bunt of the net by strapping. A winch aids in cinching up the strapping slings. If the skiff is powered, it is sometimes used to tow the fishing vessel away from the net during hauling operations. In most cases, however, the captain sets the net so that the vessel is downwind during retrieval, and towing is unnecessary. The bag of the net is held open with a wooden or metal boom (tangón) and by the skiff. Brailing squid from the net into the fish hold requires at least five men. Two men in the skiff dip the brail into the bag to fill it with squid. A man on the winch hoists the brail, and two men pull it toward the vessel while the men in the skiff push the handle. After excess water is drained off, the net is poised over the fish hold and the purse line slackened to allow the squid to fall into the hold. Loose netting is hauled by hand during the brailing operation as the weight in the bag diminishes. When transferring the catch from the net into a barge or lighter, the brail is handled from the main vessel and pushed over the net to the lighter. Most brailing is done with the sock brail, which is operated from the main vessel, similar to the method used in Southern California.

In a typical set, about 1.5 minutes are required to set the net around a school of squid. The towlines and wings are hauled aboard in about five minutes. The net is dried up by strapping in 40 minutes. Brailing requires about 2.5 minutes per ton of squid.

About 12 to 16 vessels regularly participate in the Monterey squid fishery. They range from 8 to 16 m in length and 8 to 52 tons in gross tonnage. The smaller vessels tow lighters which can carry about 25 tons of squid (Fig. 17). Most vessels have hydraulic power to operate gurdies, but do not have electric (AC) generators. None of the fish holds are refrigerated. When squid are unavailable, these vessels fish primarily for Pacific herring (Clupea harengus pallasi) and anchovy. Crew complement varies from 6 to 10 men.

The catch is landed at Monterey or at Moss Landing, located about 30 km to the north. Unloading is carried out by brailing from the hold into a chute under the pier. The chute leads to a wire conveyer belt (Fig. 18) which dewaters the squid and carries them into a weighing hopper on top of the pier. From the scale, the squid is fed by conveyer into a waiting truck which carries the squid to the processing plant.

4. COMPARISON OF FISHING METHODS

In the California squid fishery, choice of fishing methods is dictated by several factors, not all of which bear upon efficiency. Price, market demand, and processing capacity, as well as fishing regulations and traditions, are factors which determine choice of fishing methods. At Monterey methods necessitating large crew complements are feasible because of the high price paid for squid. On the other hand, despite lower prices, southern California fishermen can profitably brail 10 to 20 tons of squid per day because of the small crew required. It is not clear why these brailers have not converted to pumps. Certainly many of the vessels are capable of using a pump, but there has been a strong opposition to change. Reasons given for this opposition are the low price paid for squid, small market orders, cost of the required equipment, and doubt of the efficacy of the pump system (despite the obvious success of the lone fisherman using the pumping method). Moreover, many of the vessels maintain a crew of three men when fishing for other species, and rather than replacing one man with a pump, the captains prefer to keep the crew intact. This is because squid is usually not the principal target species for the vessels.

Purse seines are also effective, but low market demand, small processing capacity, and existence of alternate fisheries which are more attractive restrict their use. Thus catches by purse seine in southern California are usually restricted to late in the season, when squid from other sources are scarce and other fisheries are not profitable. Small catches of squid are not economical for purse seiners because of the low price and large crew complement. Mixed catches are ordinarily not possible because fish holds are not adequately separated.

The lampara net is certainly effective in catching squid in shallow water. Its only disadvantage is the large crew size required, particularly during the brailing operation. Mechanical aids, such as a pump for transferring fish into the hold, could make it possible to increase efficiency. As previously mentioned, fishing regulations prohibit the use of purse seines or attracting light in Monterey Bay.

5. FUTURE OF THE FISHERY

Although many questions regarding the populations of Loligo opalescens and the maximum sustainable yield are unanswered, it is clear that the annual catch off California can be increased substantially, if the economic conditions warrant. The chief constraint to growth of the fishery is market demand. Given a consistent and higher demand, more squid could undoubtedly be taken by the existing fleet at the traditional fishing grounds during most years. Additionally, new fishing grounds and alternative fishing methods could be developed to further increase the catch. The wide area between the southern and northern fishing grounds has remained unexploited, although squid are known to be present in substantial quantities. Probably the greatest constraint against a real expansion is that normally supply at traditional fishing grounds exceeds market demand. In years of low availability at the normal fishing grounds, lack of suitable unloading facilities hampers expansion into other areas. It should be emphasized, however, that there are no data showing that squid are available at other areas when they are scarce at the primary fishing grounds; indeed, experiences of both fishermen and researchers seem to indicate that in poor fishing years abundance of squid is low throughout California. To open up new areas which are far from existing ports, squid will have to be refrigerated or new unloading facilities constructed. A possible solution to the latter problem is the use of large diameter fish pumps, which could be used both for fishing and for offloading.

Research is needed on economics, population dynamics, distribution, and life history of Loligo opalescens in order to expand the fishery with due regard to optimum sustainable yield, economic ramifications, and the ecosystem. Areas of particular importance for management in which knowledge is lacking are possible existence of distinct groups and age composition of the catch.

Regarding fishing methods, experiments are needed to determine optimum types and intensities of lamps, with the goal of better manipulating the behaviour of squid. Alternate fishing methods - such as bottom and mid-water trawling - may prove to be fruitful in some areas or seasons, particularly with the nonspawning squid.

The fishery at Monterey can certainly be made more efficient, but existing social and economic conditions presently deter attempts at modernizing gear and methods. Light-attraction methods need to be tried to determine if quality of squid differs from lampara-caught animals. Considerable labour savings could be achieved by using pumps instead of brailing squid out of the net into the hold. However, most of the vessels are probably too small to justify installation of a pumping system.

Research presently being done by California Department of Fish and Game and the Moss Landing Marine Laboratories should provide many of the answers needed to enable a rational expansion of the California squid fishery. These studies are conducted under the auspices of the Sea Grant Program, funded by the National Oceanic and Atmospheric Administration and by the State of California.

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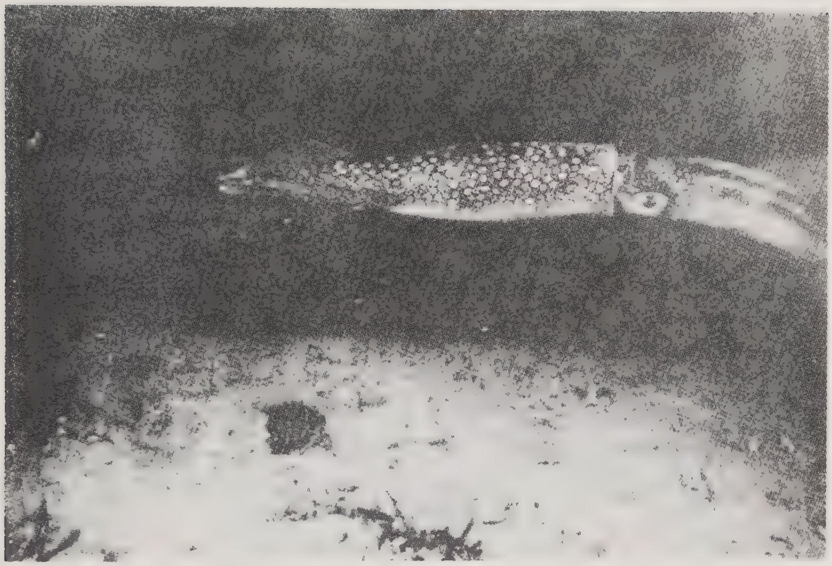

Figure 1.- Loligo opalescens. Photo credit: D. Gotshall

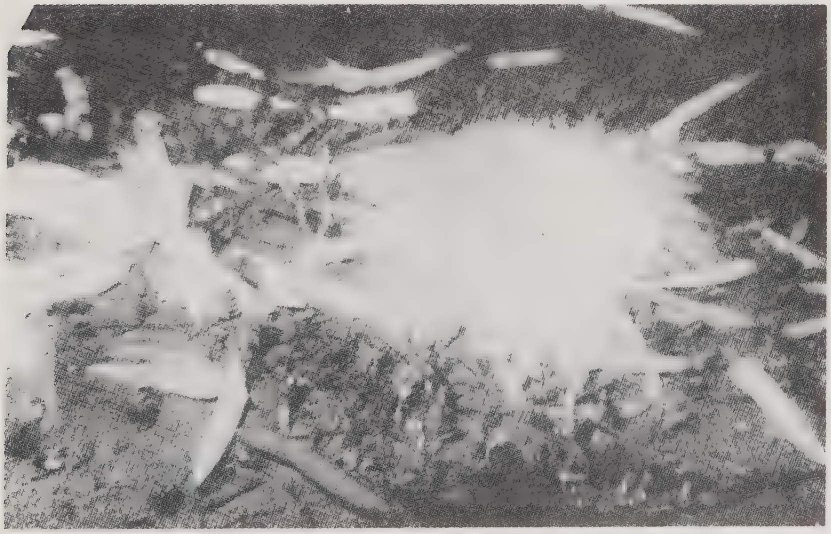

Figure 2. Aftermath of a period of spawning activity. Dead squid are shown around a cluster of eggs. Photo credit: E. S. Hobson.

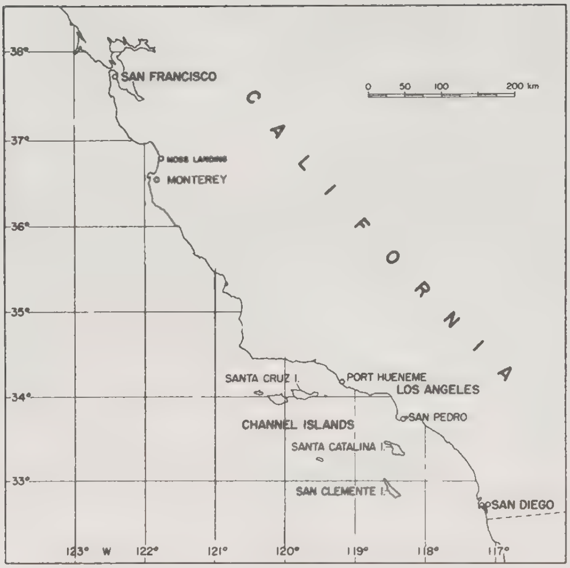
38°
37°
36°
35°
34°
33°
SAN FRANCISCO
CALIFORNIA
0 50 100 200 km
MOSS LANDING
MONTEREY
SANTA CRUZ I.
PORT HUENEME
LOS ANGELES
SAN PEDRO
CHANNEL ISLANDS
SANTA CATALINA I.
SAN CLEMENTE I.
SAN DIEGO
123° W 122° 121° 120° 119° 118° 117°

Figure 3.- Map of central and southern California. Major fishing grounds are located at Monterey and the Channel Islands.

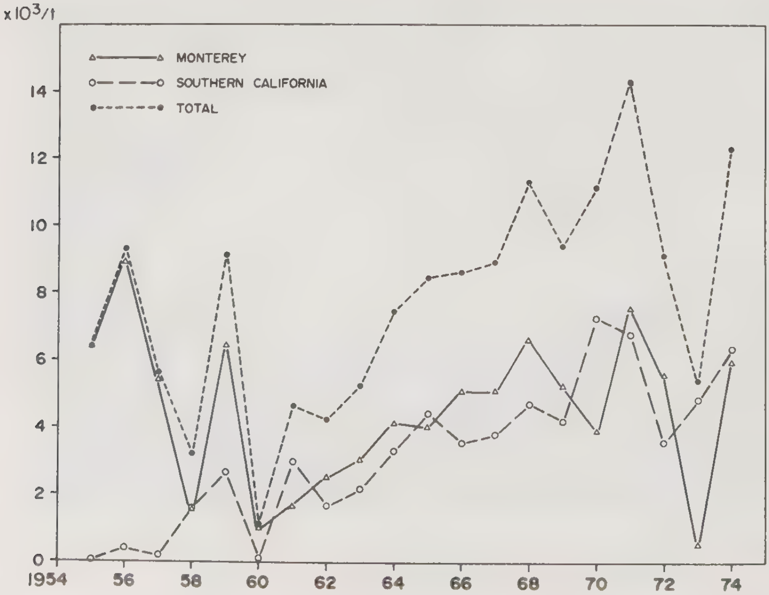

Figure 4.- Annual landings of squid at the Monterey area and southern California, 1955-1974. Data are from the Statistics Division, California Department of Fish and Game, Long Beach, California.

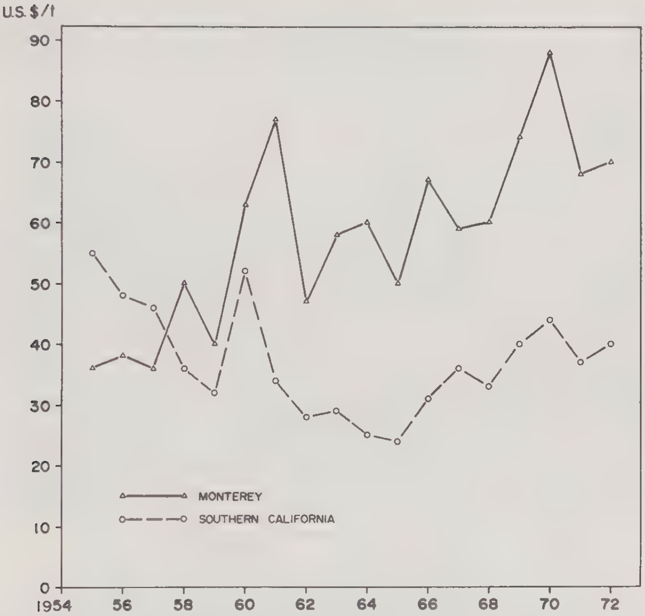

Figure 5.- Value per metric ton of squid landed at the Monterey area and southern California, 1955-1972. Data are from the Statistics Division, California Department of Fish and Game, Long Beach, California.

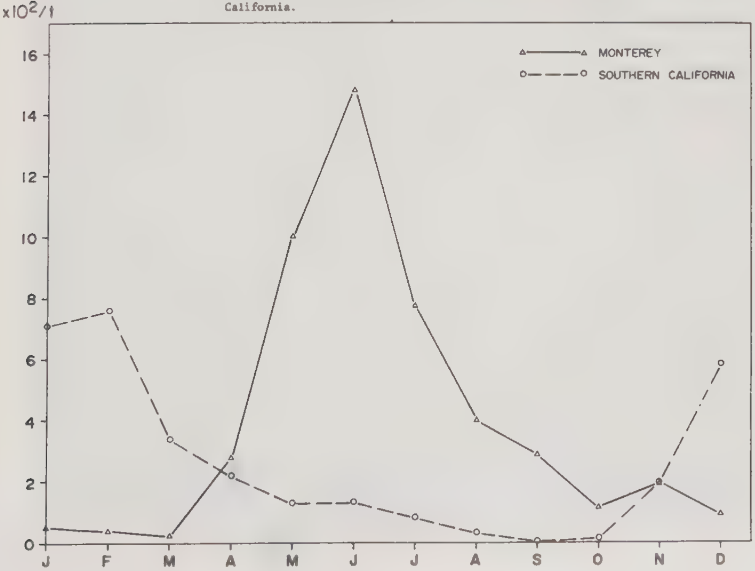

Figure 6.- Average monthly landings of squid at the Monterey area and southern California, 1955-1974. Data are from the Statistics Division, California Department of Fish and Game, Long Beach, California.

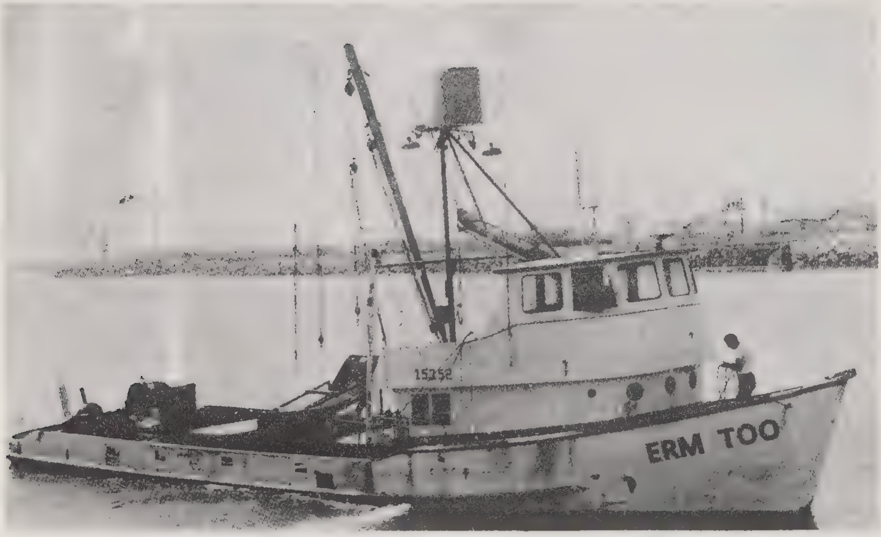

Figure 7.- Typical squid brailing vessel. Two lamps near the top of the mast are the attracting lamps.

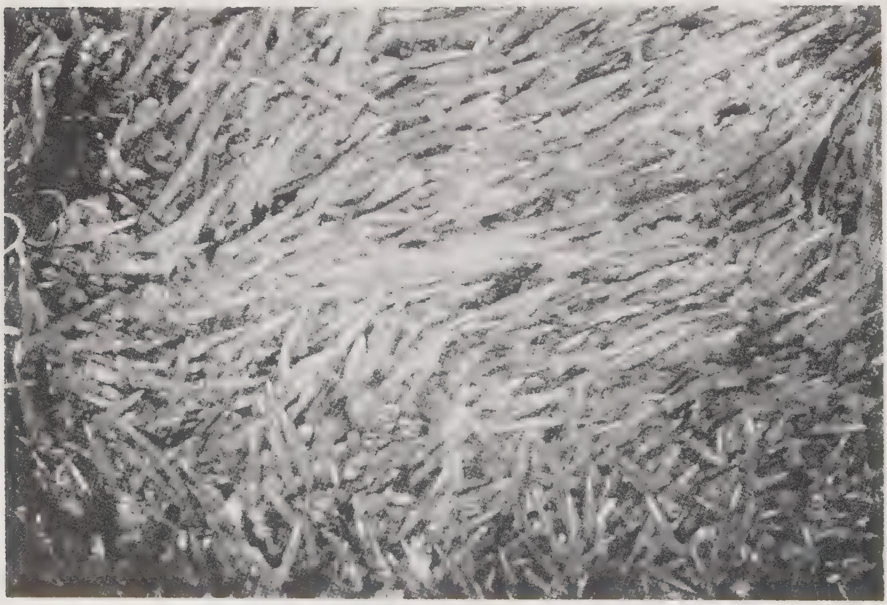

Figure 8.- A school of squid attracted to the surface and gathered under the concentrating lamp.

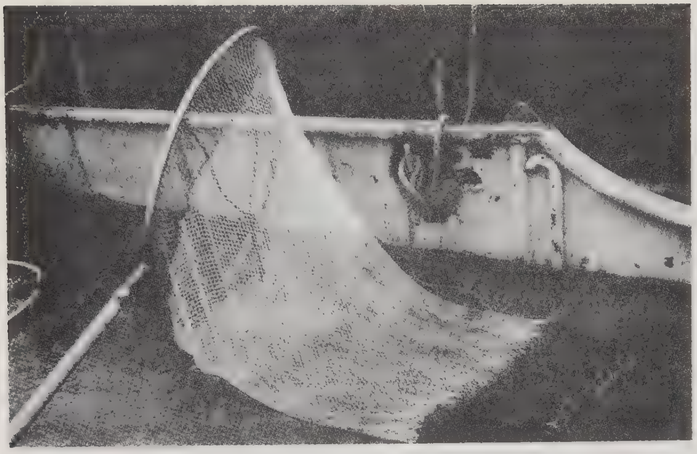

Figure 9.- A typical squid brail with a hoop diameter of about one meter. Note the purse rings at the bottom.

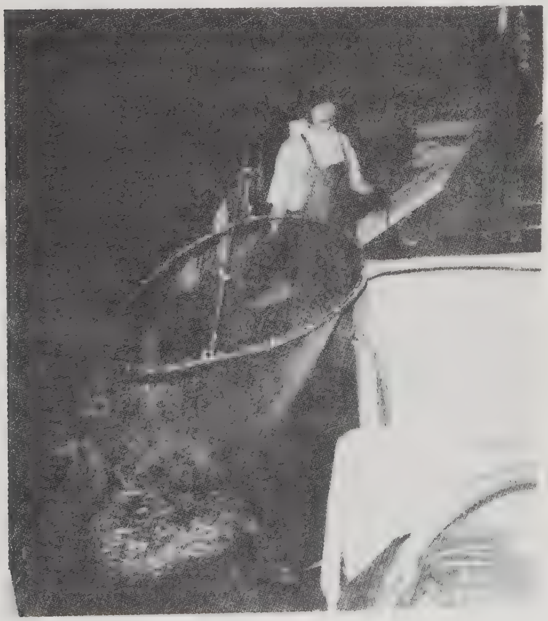

Figure 10.- Brailing squid. The brail is laid on deck to remove excess water before the squid are released into the fish hold.

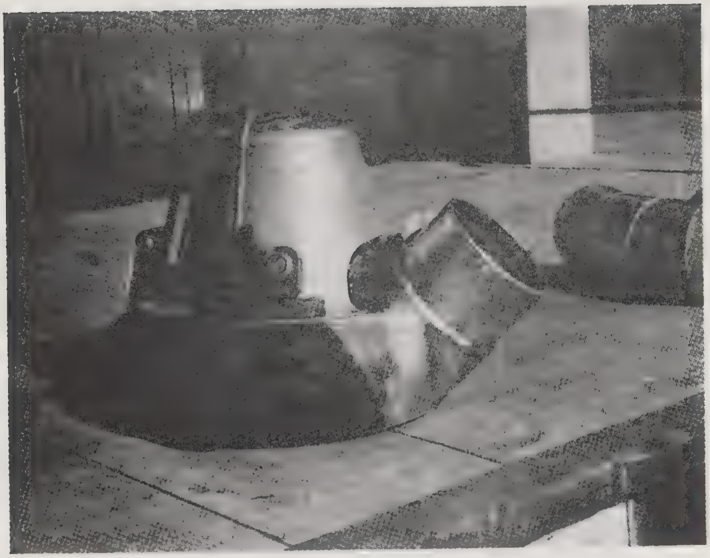

Figure 11.- Marco Model U-230 Capsulpump, side view. The entrance, not shown, is on the bottom.

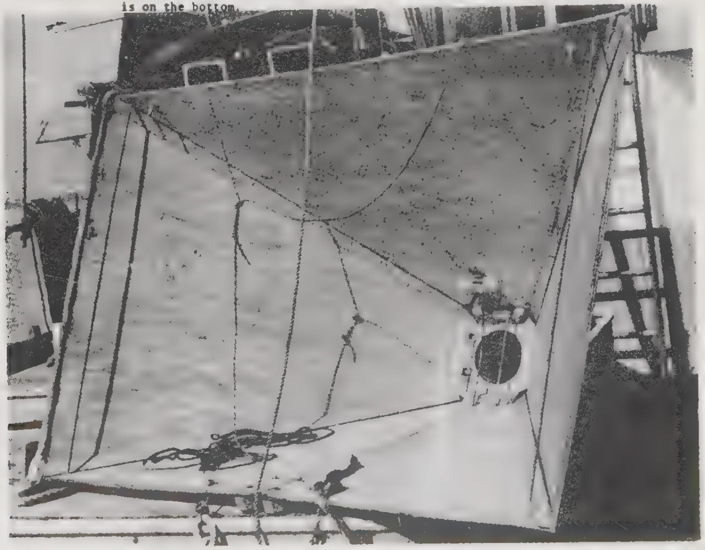

Figure 12.- Early funnel design constructed of wood and including a quartz-halogen underwater lamp.

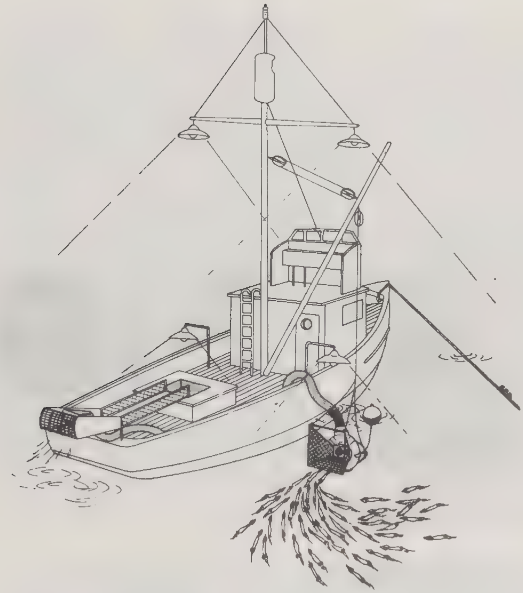

Figure 13.- Diagram of squid pumping system. Squid pass through the funnel and pump to a hose which leads to a dewatering screen.

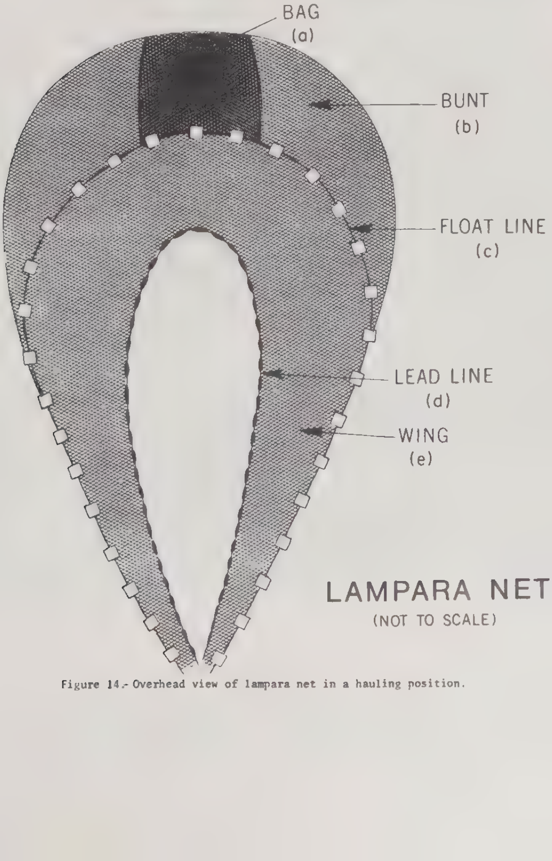
BAG
(a)
BUNT
(b)
FLOAT LINE
(c)
LEAD LINE
(d)
WING
(e)
LAMPARA NET
(NOT TO SCALE)

Figure 14.- Overhead view of lampara net in a hauling position.

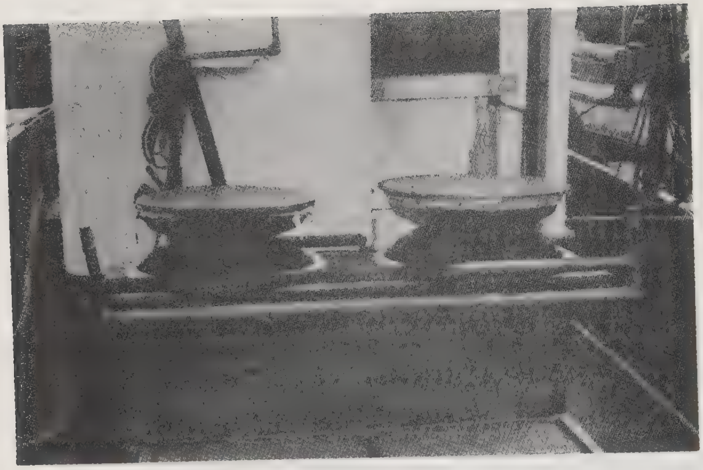

Figure 15.- Gurdies used at Monterey for hauling wings of lampara net. These gurdies are placed amidship.

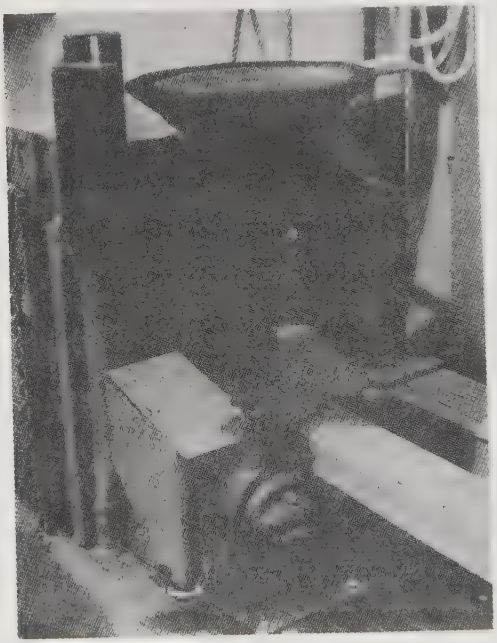

Figure 16.- Single gurdy used to pull one wing. A second gurdy, not shown, is situated near the stern of the vessel. Although most gurdies are hydraulically powered, this particular gurdy is mechanically powered.

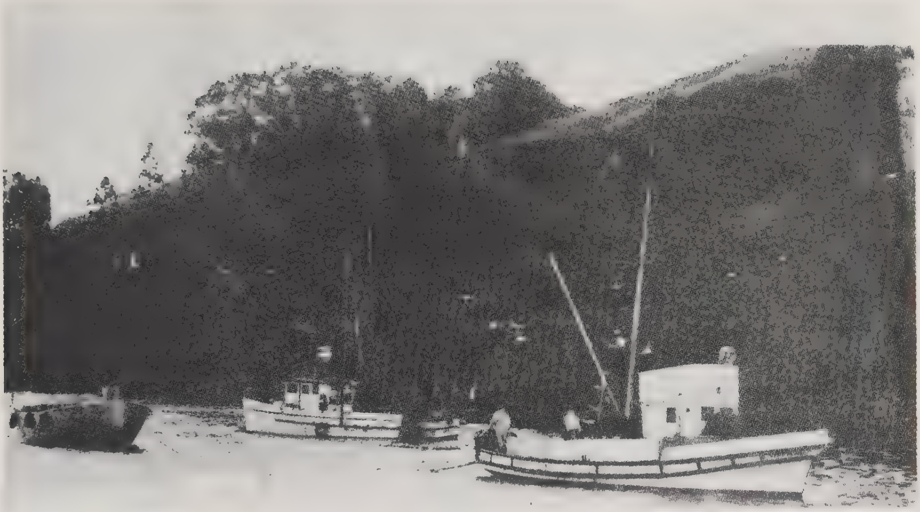

Figure 17.- Monterey lampara vessels in set. The vessel in the right foreground uses a lighter (left) to store the catch. The vessel in the background is strapping and hauling the bunt with the boom. Photo credit: J. Spratt.

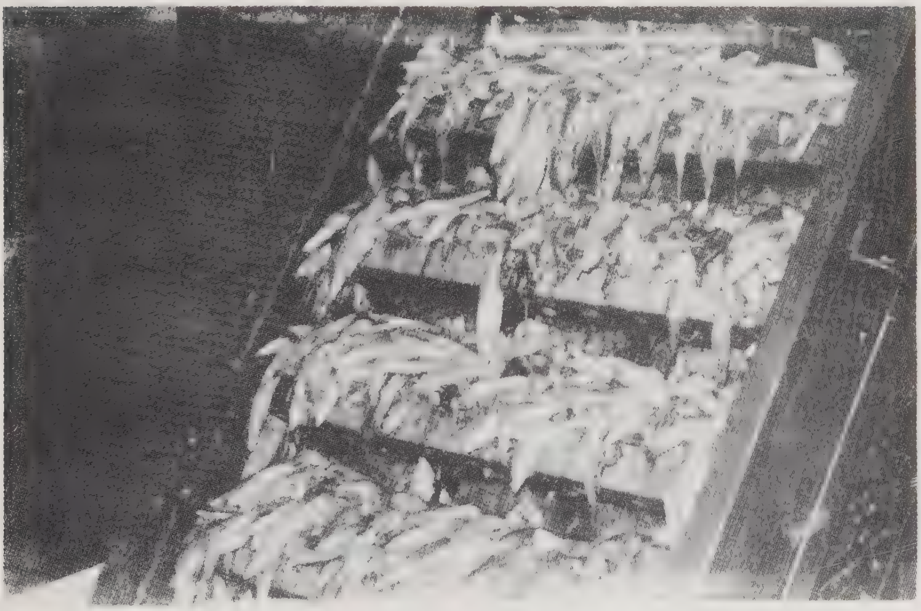

Figure 18.- Conveyer belt full of squid leading to a weighing hopper.

UPTAKE, DISTRIBUTION, AND DEPURATION OF ^{14}C-BENZENE IN NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND STRIPED BASS, *MORONE SAXATILIS*

Sid Korn,[1] Nina Hirsch,[2] and Jeannette W. Struhsaker[2]

ABSTRACT

The uptake, distribution, and depuration of water-soluble, monocyclic hydrocarbon contained in petroleum and refined products was studied in two species of marine fish. Mature northern anchovy, *Engraulis mordax*, and juvenile striped bass, *Morone saxatilis*, were exposed to sublethal concentrations of ^{14}C-benzene for 48 h. Residues in tissues exhibiting a high lipid content or representing apparent major metabolic sites were measured during the exposure and afterwards when the fish were transferred to clean seawater. Fish exhibited a rapid uptake over a wide range of benzene concentrations in the water column. Accumulation in anchovy was considerably greater than in striped bass. Results indicate that the pathway of hydrocarbons through the liver, gallbladder, intestines, and colon is a major depuration route. Residues were depurated rapidly after cessation of exposure; in striped bass tissues most residues were undetectable by 7 days.

Increased drilling, transportation, and refining of crude oils near or on coastal waters has led to the need for research on the effects of oil on estuarine biota. Considerable public concern has evolved from such occurrences as tanker spills and the Santa Barbara well blowout. However, long-term sublethal effects of low levels of oil in inshore areas may be of greater importance to marine populations than short-term lethal effects of high levels resulting from catastrophic events such as tanker spills and drilling blowouts. It is important to study the effects of chronic oil exposure on marine organisms.

Benzene is a principal aromatic oil component (up to 6.75 ppm in the water-soluble extract [Anderson et al. 1974]) that is relatively water soluble (1,993 μl/liter [Benville and Korn 1974]) and has significant effects on fishes (Brocksen and Bailey 1973; Korn et al. in press). The preceding studies demonstrated the effects of benzene on the nervous system, respiration, and growth of fish. Brocksen and Bailey showed latent effects of benzene on respiratory response lasting up to 6 days after fish were placed in clean water.

Concentrations of highly volatile monocyclic aromatics such as benzene are not thought to be very high in areas subject to chronic exposure to oil. However, measurements of monocyclic aromatics in such situations are scarce. Our preliminary measurements in San Francisco Bay indicate a maximum range from 1 to 10 μl/liter benzene in relatively unpolluted bay areas. Although the chronic levels are low, if fish accumulate benzene over field concentrations and if energy is required to metabolize, detoxify, and depurate accumulated aromatics, detrimental long-term physiological effects are possible.

Investigators such as Lee, Sauerheber, and Benson (1972); Lee, Sauerheber, and Dobbs (1972); Anderson et al. (1974); and Lee (1975) examined uptake of higher aromatics in invertebrates and fish, but no work has been done with benzene.

The fish we studied were San Francisco Bay species but also occur widely in other areas where chronic oil pollution may pose a problem. Striped bass, *Morone saxatilis*, is an important recreational species on the west and east coasts, while northern anchovy, *Engraulis mordax*, is not only a major forage fish for striped bass but also constitutes the greatest biomass of any fishery in the California Current.

The objective of this study was to determine the uptake, distribution, and depuration of benzene in these two species of fishes.

METHODS

Adult northern anchovies were obtained from a local bait dealer and acclimated under controlled

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environmental conditions comparable to those used in experiments. Juvenile striped bass were obtained from the water diversion facilities of the Bureau of Reclamation at Tracy, Calif. Fish were acclimated in 2,000-liter circular tanks for at least 2 wk before testing and fed ground squid once daily to satiation.

In all uptake studies, an appropriate number of fish (Table 1) were transferred into oval 200-liter test tanks and further acclimated for 1 wk. The number of fish per tank was limited to the number (<1g/liter) that could be maintained during a 48-h static exposure period when oxygen is a limiting factor. The 48-h static exposure period instead of an open-system constant exposure was necessitated by the expense of the ^{14}C-benzene required for a relatively large volume of water. Except for the 48-h static exposure period, a flow of 1 liter/min of filtered seawater was maintained throughout. During flow periods the salinity and temperature of the water were monitored and controlled by the seawater system components (Korn 1975), whereas temperature was not controlled during the static exposure period.

Stock benzene solutions used for dosing the exposure tanks were prepared as follows: A saturated benzene solution (1 ml benzene in 250 ml seawater) was prepared in a separatory funnel by vigorous shaking and then allowed to settle for 1 h. The resulting solution was analyzed by the gas chromatography method of Benville and Korn (1974). Next, ^{14}C (99.9% ring-labeled benzene, specific activity, 85 μCi/mmol) was mixed with another 200 ml of seawater to make a stock solution and was kept frozen until used. The saturated benzene solution was then mixed with ^{14}C stock solution to the proper specific activity, and the appropriate volume was poured into each tank and mixed by gentle stirring. After mixing, 1-ml water samples were added to a scintillator (10-ml Packard Instagel)[3] and the benzene concentration was measured. Carbon 14 counting was done on a Packard Model 2008 Tri-Carb liquid scintillation spectrometer system. Internal standardization yielded 85% counting efficiency, and all water values were corrected accordingly.

Uptake, distribution, and depuration were determined by sampling fish, rinsing them externally with methanol to remove adsorbed benzene, dissecting out tissues, weighing tissue samples (<200 mg), placing each tissue in a vial with tissue digester solution (1 ml/100 mg tissue Packard Soluene-100), and allowing 48-h digestion at room temperature. Scintillator (10-ml Packard Dimilume) was added to these samples and ^{14}C radioactivity measured. Approximate mean counting efficiencies of 60% and 67% were calculated from spiked samples and used to correct anchovy and striped bass tissue residue values respectively. Water and tissue samples yielding below 40 counts per minute were considered below the detectable limits of our system.

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Summary of experimental conditions for ^{14}C-benzene uptake and depuration tests with northern anchovy and striped bass. Salinity was 24-26‰

Species and test number	Specific activity (cpm/nl)	Initial mean benzene concentration[1] (μl/liter)	Tanks per concentration	Fish per tank	Time of tissue sampling[2] (days)	Total wet wt (g)		Type of tissue examined
						Mean	SD	
Northern anchovy:								
1	0.11	3.7	3	8	0.042, 0.125, 0.25, 1, 2	17.03	6.55	Liver, brain, gill, muscle
2a	5	0.11	4	8	0.042, 0.25, 1, 2, 4	12.93	5.04	Liver, brain, gill, muscle, gallbladder, intestine
2b	5	0.0097	4	8	0.042, 0.25, 1, 2, 4	11.70	4.74	Liver, brain, gill, muscle, gallbladder, intestine
3a	40	0.0048	4	8	0.25, 1, 2, 3, 4, 7	12.74	3.35	Liver, brain, gill, muscle, gallbladder, intestine
3b	320	0.00069	4	8	0.25, 1, 2, 3, 4, 7	13.94	4.46	Liver, brain, gill, muscle, gallbladder, intestine
Striped bass:								
4	5	0.088	9	5	0.25, 1, 2, 3, 4, 5, 6, 7, 8, 9	76.87	34.60	Liver, brain, gill, muscle, gallbladder, intestine, mesenteric fat, colon, heart, stomach

[1] Exposure to ^{14}C-benzene was static for 48 h followed by resumption of water flow for the duration. Recent analyses by gas-liquid chromatography yielded 0.00015-0.0010 μl/liter background benzene concentration in the seawater at this facility which is not included in these values.

[2] One fish per tank at each sampling time.

Water samples were taken first; then tissues were sampled until open flow was reestablished. Tissues were sampled as noted for each of the four experiments included in this report (Table 1). It is recognized that the residues reported may contain metabolites and degradation products in addition to benzene.

The original data on declining seawater concentrations of benzene during tests and on decreasing concentrations of residues in fish tissues during depuration were first analyzed with a least-squares curve-fitting computer program to determine if the hypothesized function was the best fit. Linear regression analyses were then performed on logarithmically transformed data, and regression coefficients were tested for significance of differences between slopes and a pooled regression coefficient (Snedecor and Cochran 1968).

RESULTS

There were no deaths during the tests. The benzene concentration in the seawater declined exponentially ($\hat{Y} = ae^{-0.0183X}$, where $\hat{Y}$ is concentration and X is time) during all tests. After 24-h exposure, 48-65% remained; after 48 h, 30-43% remained, at which point the water flow was renewed (Table 2).

In general, accumulation in striped bass was greatest in the gallbladder, followed by mesenteric fat, colon, intestine, liver, brain, gill, heart, stomach, and muscle (Table 3). Anchovy exhibited similar results minus the mesenteric fat, colon, heart, and stomach tissues, which were not sampled. The order of decreasing accumulation varied slightly according to experiment. The gallbladder accumulated 53.4-8,450 times the initial water concentration, while muscle accumulated 1.11-135 times the initial water concentration. Maximum concentrations were obtained in the tissues from 0.25 to 4 days after starting exposure. Mesenteric fat, gallbladder, liver, and intestine usually reached a maximum accumulation later than the other tissues.

TABLE 2.–Benzene concentration during 48-h exposure period. Exponential decline ($Y = ae^{-bX}$); coefficients for each experiment from least-squares curve fitting.

Test no.	Benzene-seawater actual initial concentration					Percentage remaining after	
	µl/liter	nl/liter	*n*	*a*	*b*	24 h	48 h
1	3.7	3,700	15	3.53	−0.1997	54	30
2a	0.110	110	16	0.104	−0.02381*	54	31
2b	0.097	9.7	16	0.094	−0.01262*	65	—
3a	0.0048	4.8	12	0.00457	−0.01983	48	42
3b	0.00069	0.69	12	0.000692	−0.01847	62	42
4	0.088	88	27	0.0991	−0.01813	65	43

*No significant difference between slopes (at $\alpha = 0.05$) except between tests 2a and 2b.

The equation $Y = ae^{-0.0183X}$ describes the exponential decline in benzene, using a pooled regression coefficent.

Accumulation in anchovies was considerably greater than in striped bass in the tissues measured in both species (Figures 1, 2; Table 3). The pattern of uptake in the gill and gallbladder was

TABLE 3.–Mean maximum concentration factors[1] in various tissues and days elapsed (numbers in parentheses) from beginning of exposure for northern anchovy and striped bass.

Species and test number	Initial mean benzene-seawater concentration (µl/liter)	Concentration factor in tissue of									
		Gill	Brain	Muscle	Fat	Heart	Stomach	Liver	Gall-bladder	Intestine	Colon
Northern anchovy:											
1	3.7	34.3 (2)	30.0 (2)	22.7 (1)	—	—	—	45.1 (1)	—	—	—
2a	0.11	41.8 (1)	41.8 (1)	10 (1)	—	—	—	54.6 (0.25)	4,360 (2)	209 (2)	—
2b	0.0097	113 (1)	113 (1)	29.9 (0.25)	—	—	—	309 (2)	8,450 (2)	505 (2)	—
3a	0.0048	7.92 (0.25)	7.5 (0.25)	5.42 (4)	—	—	—	66.7 (4)	229 (2)	60.4 (2, 3)	—
3b	0.00069	7.1 (0.25)	9.13 (0.25)	135 (4)	—	—	—	31.9 (2)	116 (3)	34.8 (2)	—
Striped bass:											
4	0.088	5.57 (1)	7.16 (0.25)	1.11 (0.25)	1.14 (0.25)	2.95 (0.25)	2.72 (0.25)	9.77 (0.25)	53.4 (2)	5.45 (0.25)	14.8 (0.25)

[1] Factor X (benzene-seawater concentration in microliter per liter) = actual nanoliters per gram mean tissue value or (benzene in nanoliters) / (tissue wet weight in grams).

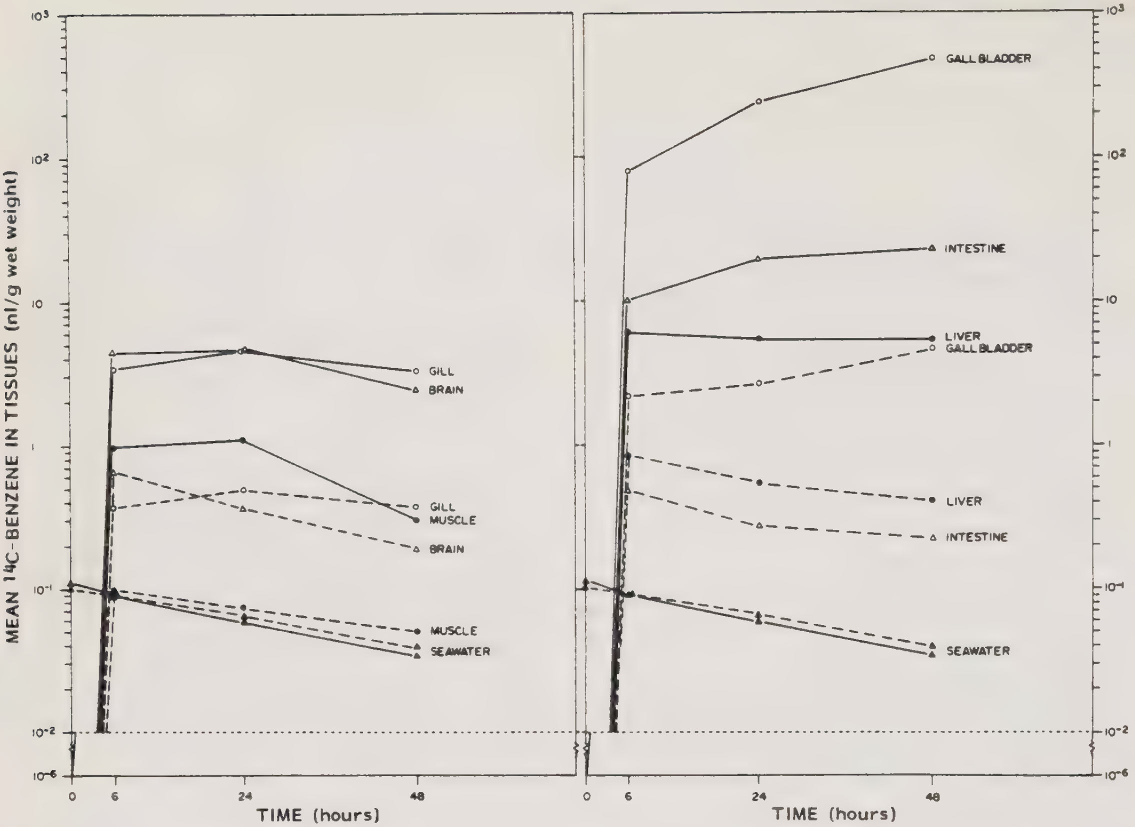

FIGURE 1.–Mean ¹⁴C-benzene uptake in tissues (nl/g wet weight) in anchovy (solid lines) and striped bass (dashed lines); sample number: three or four fish. Also shown are mean ¹⁴C-benzene concentrations in seawater in anchovy tanks (solid lines) and in striped bass tanks (dashed lines); sample number in Table 2. The concentrations on the Y-axis are calculated from total ¹⁴C radioactivity and may include metabolites of benzene.

similar between species, while in the brain, liver, muscle, and intestine, a maximum level was maintained longer in the anchovy. In both species, the greatest rate of uptake occurred in the first 6 h.

Residues were depurated rapidly after cessation of exposure (Table 4). Gallbladder, mesenteric fat, liver, and gill maintained residues the longest. Depuration appeared to occur more rapidly in striped bass than in anchovies in some tissues. In striped bass, depuration is generally described by the logarithmoc form of a power function ($\ln \hat{Y} = \ln a + b \ln X$) after cessation of exposure on day 2 until day 4 or 5 (Figure 3). Subsequently, several of the tissues showed a secondary increase and decrease in concentration. In muscle tissue, residues were undetectable 24 h after exposure ended.

DISCUSSION

Accumulation levels are based solely on radiometric analysis. This analytical technique does not distinguish between ¹⁴C-labeled benzene and derived ring metabolites. Complementary analysis by thin-layered chromatography or gas chromatography could have determined some of the actual compounds present, but it was not performed during these experiments. It is hypothesized that fish are capable of excreting and metabolizing benzene. Although there is no direct evidence, the residues reported in selected tissues may be representative of the unchanged parent benzene or associated metabolites and degradation products. Any or all of these may be toxic to fish.

Benzene and/or metabolites accumulate

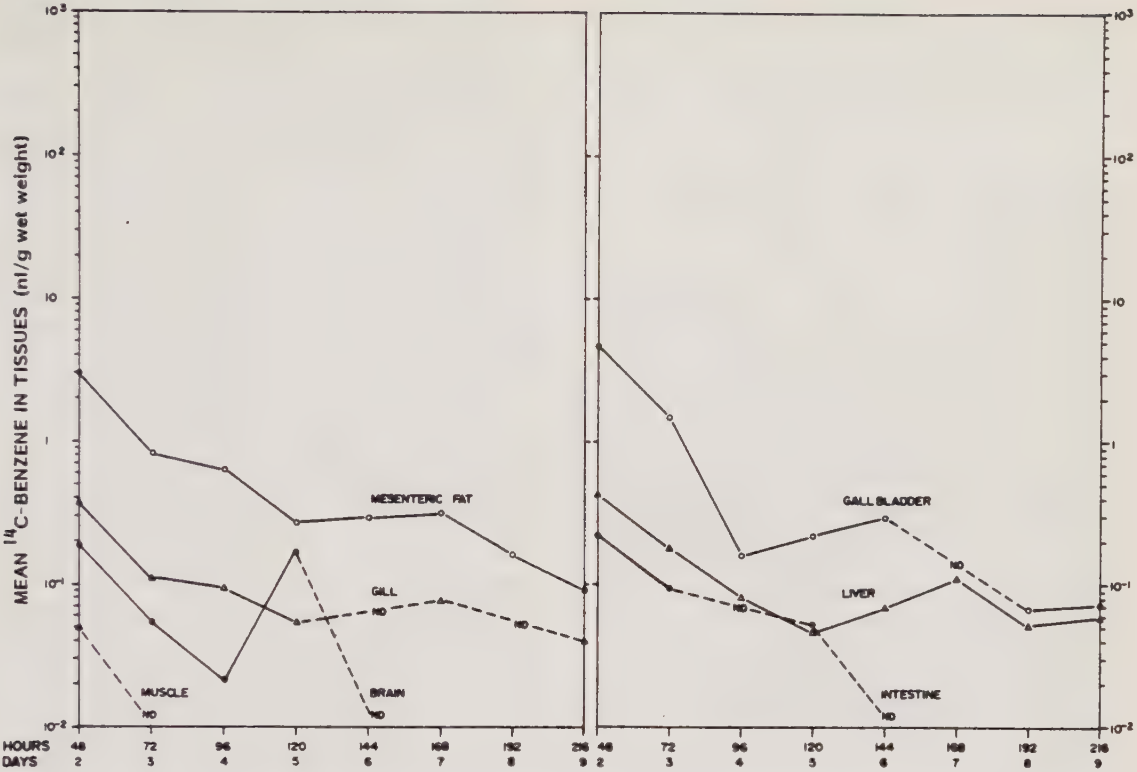

FIGURE 2.–Mean ^{14}C-benzene depuration from tissues (nl/g wet weight) of striped bass; sample number in Table 4. ND = nondetectable level (see Methods). The concentrations on the Y-axis are calculated from total ^{14}C radioactivity and may include metabolites of benzene.

predominantly in tissues that exhibit a high lipid content or represent apparent major metabolic sites. Thus, lipid-rich mesenteric fat and brain tissues had high accumulations; while liver, gallbladder, intestine, and colon (which are tissues associated with the metabolic breakdown and excretion of benzene) also accumulated benzene to higher levels (Table 3).

TABLE 4.–Percent residues[1] remaining in northern anchovy and striped bass after termination of 48-h exposure to benzene. (Sample sizes in parentheses.)

	Northern anchovy[2]		Striped bass[2]						
	Test 2a	Test 2b	Test 4						
			Days from termination of exposure						
Tissue	2	2	1	2	3	4	5	6	7
Gill	61(3)	26(2)	30(3)	25(3)	14(2)	ND[3]	21(3)	ND	11(1)
Brain	22(4)	42(1)	29(2)	11(1)	95(2)	ND	ND	ND	ND
Muscle	93(3)	ND	ND	ND	ND	ND	ND	ND	ND
Fat	—	—	28(2)	21(2)	9.0(4)	9.7(4)	11(4)	5.3(4)	3.0(2)
Heart	—	—	38(1)	ND	ND	ND	ND	ND	ND
Stomach	—	—	ND	ND	35(1)	ND	ND	ND	106(1)
Liver	70(4)	13(2)	43(3)	20(3)	11(3)	16(3)	26(3)	12(2)	14(1)
Gallbladder	69(4)	63(3)	32(4)	3.4(2)	4.7(3)	6.2(3)	ND	1.4(2)	1.3(1)
Intestine	70(4)	17(3)	42(4)	ND	24(1)	ND	ND	ND	ND
Colon	—	—	44(3)	26(2)	ND	ND	ND	ND	ND

[1] Actual nanoliters per gram tissue residues = (benzene in nanoliters) / (tissue wet weight in grams) (mean tissue residue) / 48-h mean tissue residue) (100% residue).

[2] The initial mean benzene seawater concentrations (ul/liter) were 0.11 for test 2a, 0.0097 for test 2b, and 0.088 for test 4.

[3] ND = nondetectable.

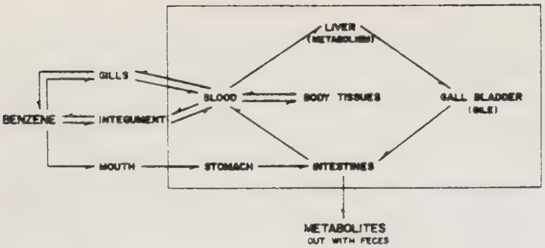

FIGURE 3.–Hypothetical pathway and distribution of benzene in fish.

Figure 3 shows a hypothetical distribution and pathway of benzene in fish which is substantiated by our results. Benzene is absorbed across the gills into the blood where, being lipid soluble, it attaches to the erythrocytes and lipoproteins (Gerarde 1960). It is then translocated via the blood to the tissues where it either accumulates or is metabolized. Parke (1968), Meyers (1970), and Lee, Sauerheber, and Dobbs (1972) described metabolism of benzene to phenol in the liver of fish and mammals. The metabolites are excreted from the liver with the bile and stored in the gallbladder. From the gallbladder the bile is excreted into the intestine and finally eliminated through the colon with the feces. Our results show high accumulation in the liver and gallbladder. Lee, Sauerheber, and Dobbs (1972) also found the gallbladder of fish to be a storage site for polycyclic aromatic compounds. Our results indicate that the pathway through the liver, gallbladder, intestine, and colon is a major depuration route. These tissues take the longest to accumulate and depurate. This is probably due to the time needed for metabolism of benzene. The gill also was one of the tissues which depurated later. Some unchanged benzene metabolites are probably excreted across the gills.

The secondary increase in ^{14}C radioactivity (days 4-7) observed after initial depuration (days 2-4) in several striped bass tissues (Figure 3) is difficult to interpret. One explanation may be that the metabolism of benzene is limited to a certain rate and that until the initial metabolism is complete, some benzene accumulates in nonmetabolic tissues and is not totally metabolized until later. The secondary increase in residues in fat and brain tissues, however, suggests that perhaps metabolites such as phenol are accumulating in the tissues for a period before they too are depurated. Additional work with uptake and depuration in herring tissues shows a similar pattern. Further research must be done to clarify this point.

The low accumulation tissues such as heart, muscle, and stomach are also low in lipid content and apparently do not directly contribute to the metabolism of benzene. Lee, Sauerheber, and Dobbs (1972) found similar results with naphthalene and benzopyrene in fish. Later work at Tiburon has demonstrated that little benzene and/or metabolites accumulate in the kidney tissue of herring. Because of this and the fact that fish in salt water excrete little urine, we feel the kidneys are not a major depuration pathway in fish from saline waters. Further study of urinary depuration is needed.

Northern anchovies are schooling fish, and they swam constantly during the tests–striped bass were more sedentary. This difference in activity might explain the higher accumulation in anchovies.

The short duration of low-level water column exposures of benzene in these experiments did not reveal obvious detrimental effects on behavior or physiology of fish. However, equilibrium accumulation levels have not been obtained because of the static exposure with decreasing benzene-water concentration. During chronic exposures, higher accumulations of benzene and toxic metabolites (such as phenol) with deleterious effects are possible. Further, because of the rapid uptake rate over a wide range of concentrations, it is conceivable that both species could accumulate significant benzene levels after brief exposure during an oil spill. The severity of effects at chronic and acute levels will depend greatly on the energy requirements of the fish and the degree of stress to which they are already subjected. Fish in spawning condition are particularly susceptible to additional stress from pollutants (e.g., spawning Pacific herring [Struhsaker[4]]). Further study of uptake in the lipid-rich mature ovaries of fish should be done.

The rapid depuration of benzene the first day after exposure ended appears to be due to metabolism and excretion via the liver-intestine route. Because of this rapid depuration, the possibility of bio-amplification in fish does not appear likely, at least after exposure from the water. Exposure from the ingestion of food organisms may result in a different metabolic process, however, and this work should be done before further conclusions are made. Our results from uptake studies with a rotifer (*Brachionus plicatilus*) (Echeverria[5]) and those of Lee, Sauerheber, and Benson (1972) and Lee (1975) with mollusks and zooplankton indicate that some invertebrates may be unable to metabolize aromatic hydrocarbons—accumulating them to very high levels and depurating them slowly. Fish feeding on such organisms may be exposed to high and potentially damaging levels of aromatics.

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Additional chronic uptake studies under continuous-flow conditions are needed. Analyses of metabolites are proceeding and will be reported later.

ACKNOWLEDGMENTS

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EFFECTS OF BENZENE ON GROWTH, FAT CONTENT, AND CALORIC CONTENT OF STRIPED BASS, *MORONE SAXATILIS*

The San Francisco Bay area is a major terminus and refinery area for crude oil, and oil-related activities in the area are expected to increase because of the Alaska pipeline and expanded drilling on the outer continental shelves of California and Alaska. The San Francisco Bay-delta region supports a number of fisheries, including the most important recreational striped bass, *Morone saxatilis*, fishery on the west coast. Information on the toxicity of aromatics in crude oil to striped bass and other fisheries is needed.

The aromatic hydrocarbon, benzene, is one of the major water-soluble components of crude oil. Anderson et al. (1974) reported 6.75 and 3.36‰ in the water-soluble fractions of south Louisiana and Kuwait crude oil standards respectively. In addition to being relatively soluble in water (1,780 ‰ – McAuliffe 1966), benzene is one of the most toxic components of petroleum.

The acute 96-h, TL-50 lethal level (10-11 μl/liter) of constant benzene exposure for juvenile striped bass was determined previously at our laboratory by Meyerhoff (1975). The objective of experiments described here was to see if sublethal levels of benzene, although not inducing death, would inhibit efficient energy utilization by the fish as measured by growth (wet weight, dry weight), fat content, and caloric content. Because the experimental period of 4 wk was relatively short, the juvenile striped bass were exposed to mean high-sublethal concentrations (3.5 μl/liter, SD 1.4; 6.0 μl/liter, SD 1.6) to determine the effects of benzene on growth.

Methods

Juvenile striped bass (mean standard length 18.1 cm, SD 2.3; mean total wet weight 3.39 g, SD 1.1) were obtained from the Tracy pumping plant operated by the Bureau of Reclamation, Tracy, Calif. After being transported by truck to our facility (Korn 1975) the fish were changed to saline water (26‰) during a 3-day period. Juvenile fish occur naturally at this salinity as well as in fresh water. The fish were acclimated for 2 wk to test conditions (salinity 26‰, temperature 15°-16°C, pH 7.8). Thirty-five fish were then placed into each of nine 80-liter fiber glass aquariums and acclimated for one more week. Halver's diet (1957) in pelleted form (5.350 kcal/g) was fed at the rate of 3% of fish body weight per day.

Benzene concentrations were maintained in three aquariums at 3.5 μl/liter benzene and in three at 6 μl/liter benzene; three others served as controls (0 μl/liter). Relatively constant benzene concentrations were maintained using the method of Benville and Korn (1974). The input of benzene-saturated air was balanced by a continuous 2 liters/min water flow through the aquariums.

Benzene concentrations were monitored daily using the gas chromatograph procedure of Benville and Korn (1974). Water quality conditions during the test were as follows: temperature, 15.2°-16.4°C; oxygen, 7.5-7.9 mg/liter; salinity, 25-26‰; pH, 7.7-7.8; ammonia, <0.5 mg/liter.

Seven fish were sampled from each aquarium at 0, 7, 14, 21, and 28 days. The animals were anesthetized with MS-222,[1] killed by severing the spinal cord, blotted dry, weighed individually, dried in a 70°C oven for 4 days, cooled in a desiccator, and reweighed. Three of the fish were then processed for caloric analyses and four for fat analyses.

Calorimetric content was analyzed by individually processing three fish in a Parr adiabatic calorimeter, model 1241.

For fat analyses, the four dried fish were blended with 150-ml MF Freon (monoflourotrichloromethane) in a high-speed blender. The mixture was poured and rinsed into a Buchner vacuum filter through No. 1 filter paper. The filtrate was put into preweighed beakers and evaporated in a hood to dryness. After reweighing the beakers, fat content was calculated.

Data were analyzed with an analysis of variance for factorial design program (BMD 02V–Dixon 1973). The independent factors of tank, week, concentration, and their interactions were tested for significance of effect on the dependent variables of wet weight, dry weight, fat content, and caloric value. Duncan's new multiple-range test (Duncan 1955; Pachares 1959) was used to determine the significant differences between means of levels for treatments found significant in the analysis of variance.

Results

Benzene concentrations varied because of fluctuations in water flow caused by particulate material clogging the valves. The high-level treatment varied from 3.6 to 8.1 μl/liter during the 4-wk test; the low-level treatment varied from 1.5 to 5.4 μl/liter. Analysis of variance of the benzene water concentration showed a significant ($P<0.01$) increase at both levels over the test period. However, the means of low (3.5 μl/liter, SD 1.4) and high (6.0 μl/liter, SD 1.6) concentrations were significantly different ($P<0.01$).

The start of benzene exposure caused pronounced hyperactivity at the high level and a moderate effect at the low level. The fish reacted by attempting to jump out of the water. Fish exposed to the high level attempted to feed but were unable to locate and consume their ration. Random jerking movements were observed when food was introduced. Fish exposed to the low level had some success locating the food, and approximately 50% of the pellets were consumed. Control fish successfully consumed all of their ration within 5 min.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

After 1 wk, feeding success on low- and high-dose fish started improving gradually. At the end of the study, the control and low-level fish fed normally, while the high-level fish consumed 50% of their ration.

Analyses of variance of wet weight, dry weight, kilocalories per gram ash-free dry weight, and percent fat between concentrations, weeks, and tanks yielded the following results (Tables 1, 2). There was a significant decrease in wet weight ($P<0.05$), dry weight ($P<0.01$), and percent fat ($P<0.01$) with increasing concentration (Table 2). Concentration levels varied significantly ($P<0.05$) (Table 1): Wet weight was less at 6.0 μl/liter than controls and did not vary significantly between 3.5 μl/liter and controls or between 3.5 and 6.0 μl/liter. Dry weight was less at 6.0 μl/liter than at 3.5 μl/liter and controls but did not vary significantly between controls and 3.5 μl/liter. Percent fat was less at 6.0 and 3.5 μl/liter than in controls. There was no significant difference in percent fat between 6.0 and 3.5 μl/liter.

There was a significant increase in dry weight ($P<0.05$) during the last week at all exposures (Table 2, Figure 1). There was no significant difference between treatments in kilocalories per gram ash-free dry weight (Table 2). The significant interaction between concentration and tank ($P<0.05$–Table 2) is a result of experimental design in which certain tanks were always at a high or low concentration. No significant variation occurred between tanks.

TABLE 1.—Mean wet wet and dry weights and fat caloric content of one control and two test groups of striped bass, *Morone saxatilis*, exposed to benzene for 4 wk.

Treatment mean concentration (μ l/liter)	Variable[2]			
	Wet weight (g)	Dry weight (g)	Fat (%)	Ash-free dry weight (kcal/g)
Control	2.7135	0.8721	39.2	6.8123
Low level (3.5)	2.6062	0.8137	34.1	6.8435
High level (6.0)	2.3951	0.7242	32.2	6.7451
Total number of fish	315	315	45	45

[1] The three treatments used three replicate tanks per treatment sampled at 0, 1, 2, 3, and 4 wk. Tests for wet and dry weights had seven fish/tank per week; tests for percent fat had four fish/tank per week; and tests for kilocalories/gram ash-free dry weight had three fish/tank per week.

[2] Duncan's new multiple-range test of differences between means of treatment levels was performed. Means grouped above with same bar are not significantly different at the 5% level. Means not grouped with same bar are significantly different at the 5% level (Duncan 1955; Pachares 1959).

Discussion

Although acclimated, fish in all treatments were stressed from crowding and insufficient water movement. This was unavoidable because space and equipment were limited. Consequently, the control fish did not grow at the same rate as similar fish held in larger tanks at this facility. In spite of these limitations, significant relative changes in growth rate and fat content did occur between exposure treatments. Wet weight, dry weight, and fat content decreased with increasing concentration as expected. This was probably due

TABLE 2.—Analysis of variance of treatment effects of benzene concentration (μl/liter), week, and tank number on wet weight (g), dry weight (g), kilocalories per gram ash-free dry weight, and percent fat of juvenile striped bass, *Morone saxatilis*.

Dependent variable and source of variation	df	Sum of squares	Mean square	*F* ratio	Probability
Wet weight:					
Concentration	2	5.511	2.756	3.16	$P<0.05$
Week	4	7.750	1.938	2.20	NS
Tank	2	3.050	1.525	1.75	NS
Concentration-week	8	11.673	0.909	1.04	NS
Concentration-tank	4	11.255	2.814	3.22	$P<0.05$
Week-tank	8	11.673	1.459	1.67	NS
Concentration-week-tank	16	15.516	0.970	1.11	NS
Within (error)	270	235.675	0.873	—	—
Total	314	302.103	—	—	—
Dry weight:					
Concentration	2	1.165	0.583	5.40	$P<0.01$
Week	4	1.232	0.308	2.85	$P<0.05$
Tank	2	0.420	0.210	1.94	NS
Concentration-week	8	0.933	0.117	1.08	NS
Concentration-tank	4	1.214	0.304	2.81	$P<0.05$
Week-tank	8	1.367	0.171	1.58	NS
Concentration-week-tank	16	2.166	0.135	1.25	NS
Within (error)	270	29.137	0.108	—	—
Total	314	37.634	—	—	—
Kilocalories per gram ash-free dry weight:					
Concentration	2	0.076	0.038	0.50	NS
Week	4	0.404	0.101	1.33	NS
Tank	2	0.284	0.142	1.87	NS
Concentration-week	8	1.177	0.147	1.93	NS
Concentration-tank	4	0.147	0.037	0.49	NS
Week-tank	8	0.667	0.083	1.09	NS
Residual (error)	16	1.222	0.076	—	—
Total	44	3.977	—	—	—
Percent fat:					
Concentration	2	383.902	191.951	13.42	$P<0.01$
Week	4	99.539	24.885	1.74	NS
Tank	2	52.878	26.439	1.85	NS
Concentration-week	8	138.843	17.355	1.21	NS
Concentration-tank	4	55.000	13.750	0.96	NS
Week-tank	8	190.733	23.842	1.67	NS
Residual (error)	16	228.929	14.308	—	—
Total	44	1,149.824	—	—	—

NS = not significant.

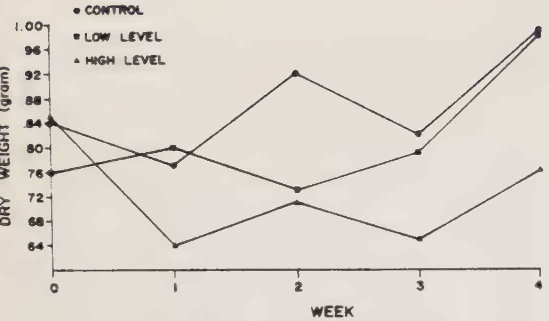

FIGURE 1.–Average weight of each of three groups of striped bass, *Morone saxatilis*, exposed to three concentrations of benzene (0, 3.5, and 6.0 μl/liter) for 4 wk. The dry weight of high-level exposure fish was significantly less ($P<0.01$) than the other two groups at the end of the first week and thereafter. The dry weight of the three groups combined was significantly higher ($P<0.05$) than in previous weeks.

mostly to impaired food localization at higher concentrations. A similar effect on the nervous system is documented by Brocksen and Bailey (1973). The energy required to metabolize benzene could also decrease efficient utilization of energy for growth and fat deposition.

There was an apparent acclimation of the fish to benzene at the low level (3.5 μl/liter) by the end of the 4-wk exposure, as reflected by the dry weight of the fish (Figure 1). After 4 wk at high level (6.0 μl/liter), fish also appeared to begin to recover from effects. This was substantiated by observations of improved feeding response in exposed fish as the experiment progressed. Nevertheless, definite effects of benzene on growth parameters were noted at 6.0- and 3.5-μl/liter levels of benzene. Although the fish may be able to adapt by metabolic detoxification and depuration of benzene and metabolites, after more prolonged periods the competitive effects on energy utilization may not only decrease growth but also increase mortality or reduce ability to withstand environmental stress.

The parameters measured in this study show effects at the low μl/liter levels. In most situations, it is unlikely that fish would be exposed to benzene above the nl/liter level except shortly after catastrophic spills. Anderson et al. (1974) obtained a concentration of several μl/liter benzene in water-soluble extracts of crude oils. In the marine environment, dilution and volatilization of benzene would probably lower the concentration of benzene rapidly. Research on effects at the nl/liter level is needed along with monitoring information on actual concentrations of benzene in chronically polluted environments. Such situations may induce a reduction in growth rate and fat deposition which would have implications in the reproductive potential of exposed species. Studies of chronic effects of low concentrations of benzene on reproduction, including fecundity, egg size, embryonic development, and larval survival, are indicated. Some of these studies have been completed at the Tiburon Laboratory and will be reported on later.

Acknowledgments

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INDUCED MATURATION AND SPAWNING OF MARINE FISH AT THE SOUTHWEST FISHERIES CENTER LA JOLLA, CALIFORNIA

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ABSTRACT

Technical details are given for spawning the following fish under controlled laboratory conditions: the northern anchovy (*Engraulis mordax*), Pacific mackerel (*Scomber japonicus*), croaker (*Bairdiella icistia*), and striped bass (*Morone saxatilis*).

INTRODUCTION

Recent successes in the sexual maturation and spawning of marine fish at the Southwest Fisheries Center, La Jolla, have been reported in the literature (Haydock, 1971; Leong, 1971). Continual refinement of maturation and spawning techniques has followed these published accounts. This paper provides an up-to-date progress report on these methods with emphasis on the northern anchovy, (*Engraulis mordax*). Preliminary details are given for other fish studied: Pacific mackerel (*Scomber japonicus*), croaker (*Bairdiella icistia*), and striped bass (*Morone saxatilis*). All of these studies have been performed to provide fish larvae for laboratory experiments (Lasker et al., 1970).

NORTHERN ANCHOVY

The spawning of anchovies in aquaria was achieved with a fixed photoperiod, 4 hours light and 20 hours darkness, and injection of hormones (Leong, 1971). Gradually, empirical changes in techniques have permitted the establishment of anchovies which are perennially sexually mature and which spawn spontaneously every day of the year. The normal spawning cycle of the northern anchovy in the Pacific Ocean is protracted with some eggs off California found from April through December, but peak spawning occurs during January, February, and March.

Basic Laboratory Techniques

Anchovies of standard length greater than 110 mm are kept in plastic swimming pools, 4.6 m in diameter, 0.72 m deep. The sea water used in these experiments is sand-filtered and irradiated with ultraviolet light (for details see Lasker and Vlymen, 1969). Each pool receives 38 liters/min. The normal pass-through flow of sea water is augmented with a centrifugal pump outside the tank which recirculates the water at 290 liters/min and provides a jet current. Anchovies normally swim against this current. Light from a 200 watt incandescent bulb provides 32 foot-candles at the water surface for 4 hours (8 a.m.-12 noon) and two, three watt bulbs give 1-2 foot-candles at the surface for the "dark" period. This slight illumination is needed during the "dark" period to prevent the anchovies from colliding with the walls of the tank. Temperature is maintained throughout the year at 15 C with the maximum allowed variation from 14.5-15.5 C. Usually about 1,000 anchovies are kept in a single tank and mature sexually from the spent condition in 2-3 months. Oregon moist chow[1] (0.6 kg/day per 1,000 anchovies) is provided to the fish with an automatic feeder[2] after a hand feeding of 0.34 kg of frozen brine shrimp.[3] Minced squid (0.9 kg/day per 1,000 anchovies) can be substituted for the brine shrimp. The tank is cleaned by vacuuming once a week.

Under these conditions all of the *E. mordax* in our tanks achieve an average gonad index (GI = (gonad wet weight/total animal wet weight) x 100) of 5; yolked eggs are present in the females and there is active sperm in the males. We collect approximately 3,000 eggs per 34,000 liters of water filtered in 15 hours but we have not determined what full production is, because the anchovies actively filter out and ingest many of the eggs, which are also lost in the overflow when filtering is discontinued. Rarely are all eggs fertilized but we have never found all eggs to be unfertilized; occasionally 100% fertilization is achieved naturally. Hatching success varies from less than 1% to over 80% (average 20%). Spawning, in our experience, occurs chiefly between 8 p.m. and midnight.

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[1] Obtained from R. V. Moore, La Conner, Washington 98257. Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

[2] Obtained from G-Z products, Inc., 2401 Gold River Road, Cordova, California 95670.

[3] Obtained from Calimar, Building 10, Brown Field Airport, Chula Vista, California 92011.

On occasion the number of eggs collected in a 15 hour period may drop off to less than 1,000 per day. Two methods usually can be used to restimulate production: a) either by cleaning the tank, or b) by raising the temperature of the sea water to 16 C overnight followed by a reduction to 15 C the following morning. Either method is effective and both have been tested on a number of occasions with duplicate test groups of anchovies.

From time to time a large number (100,000 or more) of fertilized eggs are needed. Leong (1971) described his technique for hormone injections into individual fish to insure mass spawning. Of the various hormones and injection routines tried he has adopted the following procedure: an intraperitoneal injection of 50 I.U. of human chorionic gonadotrophin (HCG)[4] in 0.1 ml Holtfreter's solution (Emmel and Cowdry, 1964) using a no. 26 hypodermic needle followed 24 hours later by an injection of 5 mg of ground salmon pituitary in 0.1 ml Holtfreter's solution (Emmel and Cowdry, 1964) using a no. 24 needle. In less than 18 hours after the second injection the anchovies spawn spontaneously; stripping was found to be unnecessary. Each injected female produces, on the average, about 10,000 eggs.

PACIFIC MACKEREL

The Pacific mackerel is a commercially important fish off California whose natural maximum spawning period ranges from June to August (Knaggs and Parrish, 1973).

Prespawning Pacific mackerel ranging in weight from 0.5-0.7 kg/fish have been subjected to a variety of photoperiods. Maturation is achieved with any light regime from a constant 4 hours of light per day to a constant 16 hours of light per day. Indoor tanks and intensity of illumination are the same as used for the anchovies (see above) but the temperature is maintained at 20 C (19.5°-20.5 C). Two hundred and fifty fish are kept in each tank. Coarsely chopped anchovies are fed to the mackerel at 6% of the estimated mackerel live weight per day supplemented with 1% of the mackerel live weight per day in Oregon moist pellets. Under these conditions fish caught in March or April 1973 matured by June 1973 when they attained GIs of 7 or 8. Although there was spontaneous spawning in June this has not occurred again although at this writing (December 1973) the GIs are still high enough for spawning, i.e., 7 to 8. The spontaneous spawning produced eggs with low hatching success, about 5%. Approximately 200 mackerel caught in a spent condition were put into a larger outdoor tank (7.3 m diameter) and experienced seasonal changes in temperature (13 C in February and March, 22 C in July and August) and illumination. Gonads matured, spawning occurred spontaneously, but differed from laboratory maintained fish, in that the gonads decreased in size once spawning was over in August.

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[4] Purchased from Sigma Chemical Co., St. Louis, Missouri 63118.

When viable eggs and sperm are desired we catheterize 0.5-0.7 kg Pacific mackerel to determine if the maximum ovum diameter is at least 0.7 mm using the technique described by Stevens (1966) and modified by May (1972).

Intramuscular injections of females with 1 mg of ground salmon pituitary in 0.1 ml Holtfreter's solution followed by 500 I.U. of gonadotrophins from pregnant mare serum (PSM)[5] 24 hours later stimulates hydration and ovulation. Eggs are obtained 12 hours later but must be stripped from the fish. HCG cannot be used with females because it causes overhydration of the ovaries and no release of eggs occurs. Males will respond to one injection of either 500 I.U. HCG or 1 mg of salmon pituitary. All of these results have been obtained by Roderick Leong of the National Marine Fisheries Service, La Jolla Laboratory, who is continuing to refine this technique with the ultimate goal of achieving spontaneously spawning animals throughout the year.

CROAKER

Haydock (1971) succeeded in maturing and spawning the Gulf Croaker at the National Marine Fisheries Service, La Jolla Laboratory, and we have used his technique at all times of the year with no extensive modifications for obtaining viable embryos. In the Salton Sea, this species usually spawns during April and May only. To summarize Haydock's work briefly: 1) To hold croakers in a sexually immature state requires 10 hours of light and 14 C temperature; 2) to mature fish in 1 month conditions must be changed to 16 hours of light and 22 C; 3) to keep mature fish at a GI of 5, maintain 16 hours of light and drop the temperature to 14 C; 4) to mature fish in 1 day after (3) above, increase the temperature to 22 C.

Continuous maintenance of fish at 16 hours light and 22 C causes eventual resorption of the gonads. Females will mature again in 2 weeks if exposed to 16 hours of light and a 22 C regime after spawning. Males usually remain running ripe under all these conditions once brought to ripeness.

The reader is referred to the doctoral thesis by May (1972) for his modifications of this technique, and for his method of assessing the state of maturity of the croakers. May spawned mature Bairdiella by using one intramuscular injection of 100 I.U. of PMS gonadotrophin in a carrier of Ringer's solution. Ovulation usually occurred 30-31 hours after the injection but eggs had to be obtained by stripping the fish.

May (personal communication) believes that not all mature Bairdiella eggs are ovulated with one injection. He says that the usefulness of the respawning method for the practical fish culturist would be very limited because the viability of the eggs on the second

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[1] Purchased from Calbiochem, Los Angeles, California.

spawning is very low, sometimes almost nil. The best procedure, according to May, is to shift once-spawned fish to cold water and short days for several months to let them resorb the old batch of eggs completely, then gradually increase light and temperature and allow them to mature again. With adequate facilities and good planning, a continuous supply of eggs can be achieved as several batches of fish at different maturity stages could be maintained simultaneously.

STRIPED BASS

The striped bass is an anadromous fish introduced to the San Francisco area from the Atlantica coast in 1879 and 1882. It spawns in the lower reaches of rivers in the spring (Roedel, 1953). Thus far Messrs. Krishan Lal and Andrew Kuljis of the California Department of Fish and Game who are collaborating with NMFS on studies of striped bass have successfully matured only males in the Southwest Fisheries Center Laboratory. Females have showed increased GI and ova diameters, but an unexplained infection causing ulcers and abdominal perforations coincided with a decline in maturity. General laboratory conditions which have given us the best results thus far are as follows: tank size and water flow are the same as used for anchovies but only 50 fish over 1.5 kg each are kept in each tank. A photoperiod of 15 hours of light at an intensity of about 10 footcandles or less (60 watt incandescent bulb) is used and the temperature is maintained at a constant 19 C. A variety of foods have been used but chiefly whole anchovies are fed ad libitum twice each day until the fish are satiated. Under this regime, males attained a GI of 10 in 6-8 weeks: females had a maximum ovum diameter of 0.75-0.8 mm and a GI of four under the same conditions. At this writing we are experimenting with suitable salinity alterations to simulate brackish conditions sought by the fish in nature. We expect this will stimulate maturation and subsequent ovulation.

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MFR PAPER 1186

Nominal Catch-Per-Unit Effort of Albacore, *Thunnus alalunga* (Bonnaterre), Caught by U.S. Jig Vessels During 1961-70

R. MICHAEL LAURS, HAROLD B. CLEMENS, and LARRY H. HREHA

ABSTRACT—Catch-per-unit effort data by time-area strata for the albacore, Thunnus alalunga *(*Bonnaterre*), fishery off the west coast of North America are presented for the years 1961-70. Results indicate that while the fishery may range from central Baja California, Mexico, to British Columbia, Canada, it is usually not continuous over this range, but rather is centered in more restricted regions in a given fishing season. Marked annual latitudinal variations in the fishery were apparent with the fishery mainly located in "southern" waters from central Baja California to San Francisco during 1961-65 and in "northern" waters off the Pacific Northwest during 1966-70. Very little variation among years in the offshore distribution of the fishery was indicated, and for the most part it was restricted to within 200-250 miles of the shore with highest catch rates frequently made within 100 miles of the coast. During "southern" fishery years, catch rates indicative of commercial concentrations of albacore were generally made 2-4 weeks earlier, during mid-June to early July, than during "northern" fishery years. Differences in the pattern of the seasonal distribution of the fishery were also apparent between "southern" and "northern" fishery years.*

A twofold variation was observed in the estimates of annual catch-per-unit effort over the 10-year period; however, relatively high catch rates with little variation were observed during the later years, 1967-70. During all of the years the concentration index was greater than 1.0, indicating that fishers tended to concentrate their effort in areas or periods where or when the average catch-per-unit effort was high.

INTRODUCTION

Catch-per-unit effort data by time-area strata are presented for the albacore, *Thunnus alalunga* (Bonneterre), fishery off the west coast of North America. They were collected by individual States and then merged and standardized. The results are unique in that they make available, for the first time, estimates of standardized catch-per-unit effort for the entire range of the fishery. This has been made possible by the cooperation of scientists from the National Oceanic and Atmospheric Administration; National Marine Fisheries Service; State of California Resources Agency, Department of Fish and Game; and Fish Commission of Oregon[1].

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Many of the statistics for the U.S. albacore fishery have been published separately by the individual States (Clemens, 1955; Ayres and Meehan, 1963; Clemens and Craig, 1965; Meehan and Hreha, 1969; and Hreha, 1974). In this paper, data collected by the States during the years 1961-70 have been combined and uniformly standardized to provide additional information about the entire range of the fishery and to take into account any coast-wide variation in the characteristics of the fishing vessels, of the geographical and seasonal nature of the fishery, or of other factors which may influence estimates of nominal fishing effort.

SOURCE OF INFORMATION

The information about catch localities and nominal fishing effort was obtained from logbooks and from interviewing fishers on the waterfront. A voluntary logbook system has been used by the California Department of Fish and Game since 1954 (Craig, 1963), and information from both logbooks and interviews was available for albacore landed in California. Information for albacore landed in Oregon was available from interviews prior to 1967 and from interviews and voluntary logbooks from 1967-70. The number of such records used for standardizing the catch rates is summarized by year and time period in Table 1. Only statistics from albacore jig boats were dealt with because there were insufficient data from bait boats. Jig boats land approximately 75 percent of the annual U.S. commercial albacore catch (Clemens and Craig, 1965). The total logged jig boat catch was roughly 30 to 40 percent of the total jig boat landings.

METHODS

Great care was taken by the individual States to insure confidentiality of the records of individual fishing vessels. This was done by removing from the records the name of each vessel and any identification numbers which could be traced to it and by assigning a code number which was kept constant each year for a given boat.

The basic data included date, number of fish caught, 1° quadrangle

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[1] The Fish Commission of Oregon has since been incorporated into the Oregon Department of Fish and Wildlife.

Table 1.—Combined number of logbooks and interview records available from albacore jig vessels for determining standardized catch rates.

Year	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970
1-15 June	2	3	4							
16-30	232	409	40	48		3	3		16	
1-15 July	1,126	1,902	1,320	1,328	459	226	100	2	207	274
16-31	885	2,215	1,266	2,075	1,303	688	811	1,260	1,646	891
1-15 August	599	1,581	1,650	1,415	1,184	760	777	1,156	1,723	1,407
16-31	305	1,177	1,027	867	1,001	478	751	1,131	1,171	1,049
1-15 September	282	945	725	647	871	321	487	610	556	960
16-30	304	451	442	652	754	309	278	659	656	625
1-15 October	107	469	310	462	506	246	74	495	304	381
16-31	52	188	194	303	386	96	78	307	381	194
1-15 November	11	17	65	197	191	33	8	41	238	91
16-30			16	47	29	6		8	137	28
1-15 December									66	1
16-31									4	
Year (season) total	3,905	9,357	7,059	8,041	6,684	3,166	3,367	5,669	7,105	5,901

within which vessel operated, boat length, gear type, and often sea surface temperature. Since the data were in several forms—magnetic tape, computer cards, handwritten listings, etc.—and in various formats, they were first put into a common format and on to magnetic tape. Data from individual States were then merged and checked by computer for duplication of records. The latter was done by searching to determine if there was more than one record, for the same day at the same location, of identical catches of albacore by boats of the same length. If so, which was true in only a small number of cases, duplicates were omitted and a final basic data tape was prepared.

A modified version of the computer program FPOW (Berude and Abramson, 1972) was used in the standardization of the nominal fishing effort within each year[2]. The theoretical development and operating characteristics of the FPOW program are described in Fox (1971). The basic model assumed in the program is:

$$C_{ij} = q_i f_{ij} \bar{P}_j \epsilon_{ij}$$

where C_{ij} is the catch of the i^{th} fishing treatment in the j^{th} time-area stratum, q_i is the catchability coefficient of the i^{th} treatment, f_{ij} is the amount of fishing effort expended by the i^{th} treatment in the j^{th} time-area stratum, $\bar{P}_j$ is the average population size in the j^{th} time-area stratum, and ϵ_{ij} is assumed to be a log-normally distributed random variable. It is assumed that: 1) effort is measured such that within each treatment q_i is constant, 2) the units of effort operate independently, and 3) there is no interaction between treatments and time-area strata.

A preliminary analysis indicated differences in fishing power among 1) vessel length, 2) time fished during the season, 3) geographic area of fishing, and 4) years. Although fishing power in reality is probably a continuous function of vessel length, in order to estimate relative fishing power, it is necessary to group the data into strata such that 1) within each class the catchability may be assumed constant, 2) the probability of isolation will be minimized, and 3) sufficient data for analysis will be available in each group.

Following these criteria, the fishing vessels were assigned to length classes, and a separate class was established for each 10-foot increment in length. For each vessel length class, catch and effort data for each year were accumulated by 3° latitude-longitude quadrangle and by 15-day period. Fishing power coefficients were then derived for each vessel length class. Statistically significant differences in fishing power were found among the several length classes and nominal fishing effort for all was standardized in terms of effort of a 45-foot jig boat, which is approximately the median vessel length for the albacore jig fleet.

In addition, apparent geographical and seasonal differences in fishing power were found. Paucity of the data on a coastwide basis precluded rigorous statistical analyses. However, subjective evaluation of the results indicated an apparent need to stratify the fishery in geographic areas, 1) north and 2) south of lat. 38°N (about San Francisco), and to stratify the fishing season into 1) early-season consisting of the months June, July, and August, and 2) late-season consisting of the months September, October, and November. To minimize the geographical and seasonal effects in the calculation of the overall catch-per-unit effort, four sets of fishing power coefficients were calculated, i.e., early-north, early-south, late-north, and late-south, for each vessel size class. The four sets of fishing power coefficients for each vessel size class are given in Table. 2.

In order to examine spatial-temporal variations in the distribution of the albacore fishery and to study fish-ocean relationships, it was desirable to derive estimates of the catch-per-unit effort on a 1° quadrangle basis. Estimates of the mean catch-per-unit effort were computed by a 15-day period and by a 1° quadrangle, applying the appropriate fishing power coefficients as follows:

Where i = region (1 = north,
2 = south)
j = season (1 = early,
2 = late)
k = vessel length class
(1 = 30,
2 = 40, . . .)
l = locality, 1° square.
Let f_{ijk} = fishing power coefficient for k^{th} vessel class in ij^{th} stratum
C_{ijkl} = catch of k^{th} vessel class in l in ij^{th} stratum
e_{ijkl} = nominal effort of k^{th} vessel class in locality l in ij^{th} stratum
$C_{ij\cdot l} = \sum_k C_{ijkl}$
$E_{ij\cdot l} = \sum_k e_{ijkl} f_{ijk}$.

Then the standardized catch-per-unit effort, in terms of a 45-foot jig boat for a 1° quadrangle l will be

$$C_{ij\cdot l} / E_{ij\cdot l}$$

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[2] Standardization procedures were carried out under the direction of William Fox with assistance by T. Mulitauaopele and J. Zweifel, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

and average catch-per-unit effort calculated from total catch and total effort over all strata will be

$$C/E = C..../E.... = \Sigma_i \Sigma_j \Sigma_l C_{ij \cdot l} / \Sigma_i \Sigma_j \Sigma_l E_{ij \cdot l},$$

while the average of all catch-per-unit effort for all vessel classes and time-area strata will be

$$C/E = \Sigma_i \Sigma_j \Sigma_l C_{ij \cdot l} / E_{ij \cdot l} / N,$$

where N = number of strata.

The estimates of mean catch-per-unit effort by 15-day period and by 1° quadrangle are given in Figures 1 to 10. We emphasize that the catch rates presented in the figures are based on data only from those vessels for which logbooks or interviews were available; however, we assume they are representative of the entire fleet of jig boats. Further, we wish to point out that 1) the catches were not evenly distributed within the time periods, and 2) the schools of albacore were not uniformly distributed throughout each 1° quadrangle.

Table 2.—Fishing power coefficients for each vessel size class for early season north of lat. 38°N, late season north of lat.38°N, early season south of lat. 38°N, and late season south of lat. 38°N.

Vessel size class	Early north	Late north	Early south	Late south	Vessel size class	Early north	Late north	Early south	Late south
1961					1966				
25	—	—	—	—	25	—	—	0.430	—
35	—	—	0.572	0.622	35	0.773	0.241	0.743	0.650
45	1.000	1.000	1.000	1.000	45	1.000	1.000	1.000	1.000
55	0.574	1.891	0.986	0.733	55	0.929	1.095	0.701	1.328
65	—	—	0.807	0.695	65	1.242	0.717	1.193	0.957
75	—	—	1.078	—	75	1.098	—	0.091	0.711
85	—	—	—	—	85	0.612	—	0.927	—
95	—	—	—	—	95	—	—	—	—
105	—	—	—	—	105	—	0.116	—	2.287
1962					1967				
25	—	—	—	—	25	—	—	—	—
35	0.718	1.520	0.864	0.948	35	0.492	0.930	0.794	0.722
45	1.000	1.000	1.000	1.000	45	1.000	1.000	1.000	1.000
55	0.737	0.566	1.191	1.032	55	0.980	1.379	0.981	—
65	0.713	0.822	0.993	0.971	65	0.906	0.468	1.169	0.915
75	1.617	0.624	—	—	75	0.863	0.242	—	—
85	—	—	—	—	85	1.131	0.505	0.893	0.135
95	—	—	—	—	95	—	—	—	—
105	0.663	—	—	—	105	—	—	—	—
1963					1968				
25	—	—	0.219	—	25	—	—	—	—
35	—	1.074	0.461	0.386	35	0.675	0.594	1.081	0.493
45	1.000	1.000	1.000	1.000	45	1.000	1.000	1.000	1.000
55	—	0.829	0.936	0.978	55	0.895	0.663	0.505	0.839
65	—	0.575	0.767	0.612	65	0.821	1.213	0.289	0.438
75	—	0.949	0.793	—	75	0.980	1.174	1.810	0.724
85	—	—	—	—	85	0.597	—	—	—
95	—	—	—	—	95	1.327	—	—	—
105	—	0.657	0.370	—	105	0.995	0.593	—	0.454
1964					1969				
25	—	—	0.449	0.114	25	—	—	—	—
35	0.332	0.561	0.616	0.425	35	0.941	0.882	0.606	0.893
45	1.000	1.000	1.000	1.000	45	1.000	1.000	1.000	1.000
55	0.862	1.210	0.814	1.089	55	1.103	1.197	0.591	0.667
65	0.599	0.854	0.909	0.606	65	0.988	0.443	1.877	0.822
75	—	1.428	0.387	—	75	1.260	0.459	—	0.975
85	—	—	1.630	0.217	85	1.372	—	—	—
95	—	—	—	—	95	—	—	—	—
105	—	0.954	0.817	0.612	105	0.819	—	0.567	—
1965					1970				
25	—	—	0.351	0.090	25	—	—	—	—
35	0.490	0.857	0.566	0.483	35	0.427	0.903	0.641	0.677
45	1.000	1.000	1.000	1.000	45	1.000	1.000	1.000	1.000
55	0.667	1.243	1.032	0.578	55	0.992	2.888	0.761	0.766
65	0.670	1.394	1.227	0.906	65	1.069	1.003	0.878	1.170
75	—	—	—	1.001	75	1.014	1.747	0.532	0.820
85	—	—	—	—	85	0.443	—	—	—
95	—	—	—	—	95	—	—	—	—
105	0.731	2.638	0.597	0.798	105	0.162	0.335	0.402	0.781

RESULTS

Charts of catch-per-unit effort in terms of a 45-foot jig boat by 15-day period and 1° quadrangle are given in Figures 1-10. Some general comments will be made concerning the data given in the figures, including 1) the annual latitudinal variation in the distribution of the fishery, 2) the offshore distribution of the fishery, and 3) the seasonal development of the fishery. A detailed analysis of the charts will not be given. Readers can draw their own conclusions depending on their intended use of the charts. Estimates of the mean standardized catch-per-unit effort and concentration index by years are also presented.

Annual Latitudinal Variation in the Distribution of the Fishery

Although the jig fishery for albacore ranged from central Baja California, Mexico, to British Columbia, Canada, usually it was not continuous or evenly distributed over this area (Figs. 1-10). Instead, fishing was centered in relatively restricted regions which varied in location both within and between seasons. Marked annual latitudinal variations in the location of the center of the fishery are also clearly evident in the figures. For example, during the period 1961-65 most fishing took place south of San Francisco. In these "southern" waters the geographic range of the fishery was greater and the catch rates usually higher than to the north (Figs. 1-5). By 1966, however, a major part of the fishery had shifted to "northern" waters above San Francisco, where the extent of the fishery and the catch rates were much greater than to the south—these conditions persisted through 1970 (Figs. 6-10).

Annual variations in location of the albacore fishery have been observed over at least the past three decades. They are indicated in Figure 11 (from Laurs, 1971), which gives the percentage of the west coast albacore tuna catch taken north of San Francisco for the years 1938-70. According to Laurs et al. (1974), based on unpublished work by James Renner[3], these variations appear to be related to marine environmental conditions during spring months in the offshore waters through which albacore presumably pass during their migration from the central Pacific into the west coast fishing grounds.

Variation in the location of the fishery has affected the amount of albacore landed in the individual Pacific

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[3] Southwest fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. commun.

Coast States. For example, during the 1961-65 "southern" fishery years, landings in California ranged from 23.22 to 48.86 million pounds, while landings in Oregon ranged from 3.25 to 12.12 million pounds. However, during the 1966-70 "northern" fishery years, landings in California decreased, ranging from 14.72 to 29.93 million pounds while landings in Oregon increased, ranging from 17.68 to 37.75 million pounds. Albacore landings in Washington also were highest when the fishery was centered to the north (Table 3).

Table 3.—Amount of albacore landed by state (in millions of pounds)[1].

Year	Calif.	Oreg.	Wash.	Total
1961	29.12	3.25	0.46	32.83
1962	36.62	8.95	0.37	45.94
1963	48.86	11.40	0.53	60.79
1964	42.55	4.46	1.05	48.06
1965	23.22	12.12	1.87	37.21
1966	18.19	17.68	1.10	36.97
1967	17.86	29.24	1.24	48.34
1968	15.08	37.75	3.05	55.88
1969	14.72	29.83	3.56	48.11
1970	29.93	21.80	4.39	56.12

[1] Sources of information: Power (1963), Powell and Lyles (1964), Lyles (1965, 1966, 1967, 1968, 1969), U.S. Department of Commerce (1971), and Wheeland (1972, 1973).

The Offshore Distribution of the Fishery

Little variation was apparent in the offshore distribution of the albacore fishery (Figs. 1-10). Most fishing occurred within 200-250 miles of shore, with the highest catch rates frequently made within 100 miles of the coast. However, there was generally a strip of varying width along the coast which was void of albacore catches. The width of this strip was often greatest off northern California and Oregon where it sometimes extended 50 or more miles offshore.

According to several authors (Clemens, 1961; Pearcy and Muller, 1969; Flittner, 1970; Panshin, 1971; Laurs, 1973; and others), albacore may avoid nearshore waters off the coast of North America because water temperatures there are below those considered optimal for albacore (Laevastu and Rosa, 1963). These cool coastal waters result from coastal upwelling (Smith, 1968) and the nearshore areas which were devoid of albacore catches extended the farthest offshore where upwelling has been found to be strongest (Bakun, 1973).

Seasonal Development of the Fishery

General information about the seasonal development of the albacore fishery and its year-to-year variations can be obtained from the charts of catch-per-unit effort. However, since there is a complicated interplay of numerous factors (including availability of albacore, socioeconomic, weather, oceanographic conditions, etc.) that may influence the catch rates, care should be exercised if the charts are used to evaluate such events as the beginning or end of the fishery for specific years, within-season variations, etc.

It can be seen in Figures 1-10 that the albacore jig fishery is seasonal, generally lasting from July through October, although some catches were made as early as the first half of June (Figs. 2 and 3) and as late as mid-December (Fig. 10). During "southern" fishery years, catches indicative of commercial concentrations (catch rates of about 100 fish per day) were often made beginning in mid-June to early July (Figs. 1-5). This is about 2-4 weeks earlier than during the "northern" fishery years when significant catches usually were not made until after mid-July (Figs. 6-10).

There were also differences in the pattern of the seasonal distribution of the fishery between "southern" and "northern" fishery years. During most "southern" years a single fishing center was observed (Figs. 1-5). It expanded, generally moved northward, and then contracted during the fishing season. The fishery usually began between northern Baja California and southern California, expanded northward up the coast during the late summer and early fall months to northern California or Oregon, and then receded southward during the late fall to off central California where the fishing season usually ended. A different pattern was observed during most "northern" fishery years (Figs. 6-10) when two widely separated fishing areas prevailed from the beginning of the season through the late summer months. One of these areas was off the Pacific Northwest and one off southern California, with the former occupying a larger geographic area and having generally higher catch rates than the latter. By early fall, the southern area had shifted northward and the northern area southward, forming a single area off central California where the fishing season usually ended in the late fall.

Annual Standardized Catch-Per-Unit Effort

Estimates of annual standardized catch-per-unit effort were derived to provide information on the trends in albacore fishing success. These estimates were based on data for the period 1 July to 31 October and were derived in two ways: 1) the total catch divided by the total standardized effort,

$$CPUE_1 = \Sigma C / \Sigma f, \qquad (1)$$

and 2) the sum of the *CPUE* for each time-area stratum divided by the number of strata,

$$CPUE_2 = \frac{1}{n} \Sigma C/f \qquad (2)$$

where C denotes catch, f denotes nominal standardized effort, and n denotes the number of time-area strata.

Estimates of the annual standardized catch-per-unit effort based on Equations (1) and (2) above are given in Table 4 and Figure 12.

A two-fold variation in the annual catch-per-effort of albacore was observed during 1961-70. The ratio of averages *CPUE* statistic ranged from 69.24 to 136.99 fish per day, and the average of ratios *CPUE* statistic ranged from 61.24 to 119.03 fish per day. Both estimates of catch-per-unit effort were relatively low in 1961 and 1964-66, and high in 1962-63 and 1967-70 (Fig. 12).

Annual Concentration Index

To obtain a measure of the extent to which the albacore jig fleet has been successful in concentrating nominal effort in areas where or when average catch-per-unit effort has been high, computations were made for each year of the concentration index (Gulland, 1955). This index is the ratio of the ratio of averages *CPUE* statistic, Equation (1), to the average of ratios *CPUE* statistic, Equation (2):

Table 4.—Annual values of standardized fishing effort, logged catch, catch-per-unit effort, and concentration index for the U.S. albacore jigfishery during 1961-70.

Year[1]	Effort[2]	Catch[3]	[4]$CPUE_1$	[5]$CPUE_2$	Concentration index
1961	3,542.2	245,438	69.24	61.24	1.13
1962	9,236.4	1,151,957	124.72	112.55	1.11
1963	5,797.7	772,474	133.24	119.03	1.12
1964	7,102.8	697,331	98.18	76.26	1.29
1965	6,042.5	547,063	90.54	63.25	1.43
1966	3,019.4	276,148	91.46	62.27	1.47
1967	3,249.9	411,046	126.48	90.14	1.40
1968	5,322.7	729,165	136.99	93.97	1.46
1969	6,529.6	754,236	115.51	72.49	1.59
1970	5,308.0	680,083	128.12	88.12	1.45

[1] For period 1 July to 31 October.
[2] Standardized boat-day of logged effort.
[3] Number of logged fish.
[4] Ratio of averages *CPUE* derived using Equation (1).
[5] Average of ratios *CPUE* derived using Equation (2).

$$Ig = [\Sigma C/\Sigma f]\,[1/n\Sigma C/f]^{-1}.$$

During each year the concentration index (*Ig*) was greater than 1.0, ranging from 1.11 to 1.59 (Table 3). The values of *Ig* fall into two categories 1) one for the years of 1961-63 and 2) another for the years 1965-70. The values in the secondary category are higher than those in the first, and within each category the values are very stable. These results indicate that 1) each year albacore fishers tended to concentrate their effort in areas or period having a high average catch-per-unit effort presumably on relatively high densities of available albacore, and 2) they were relatively more successful in doing so during the years 1965-70 than during 1961-64.

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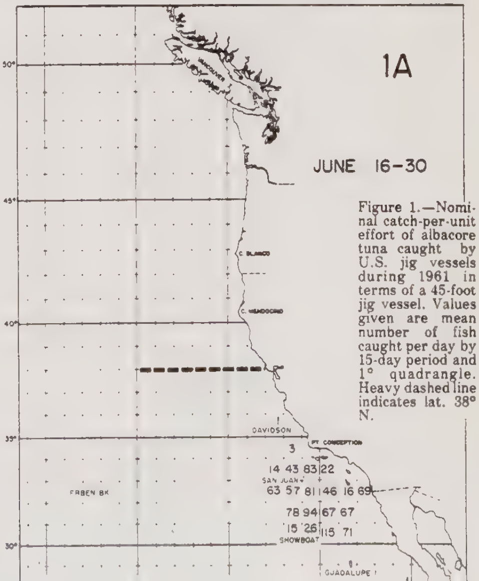
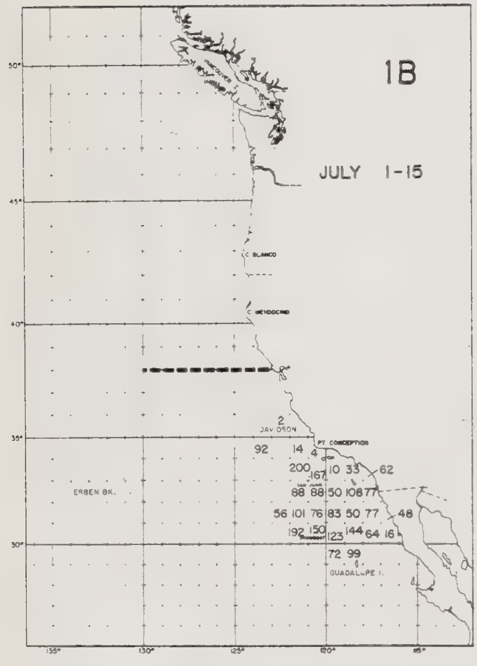


Figure 1.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1961 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.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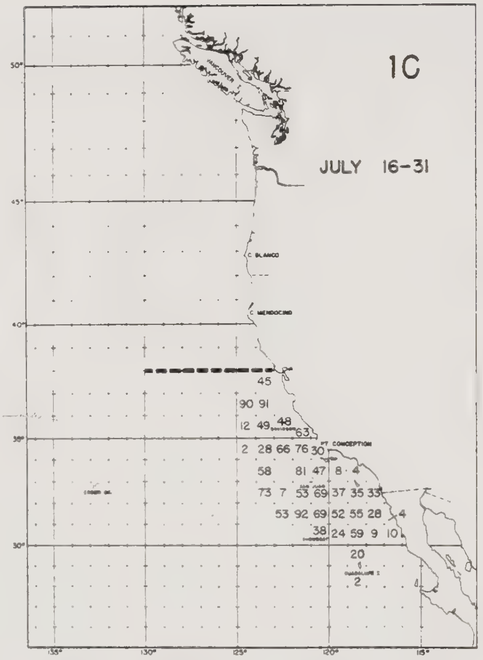
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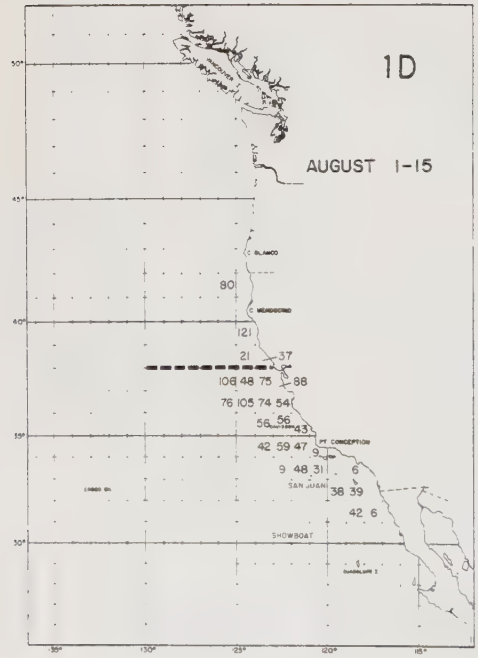
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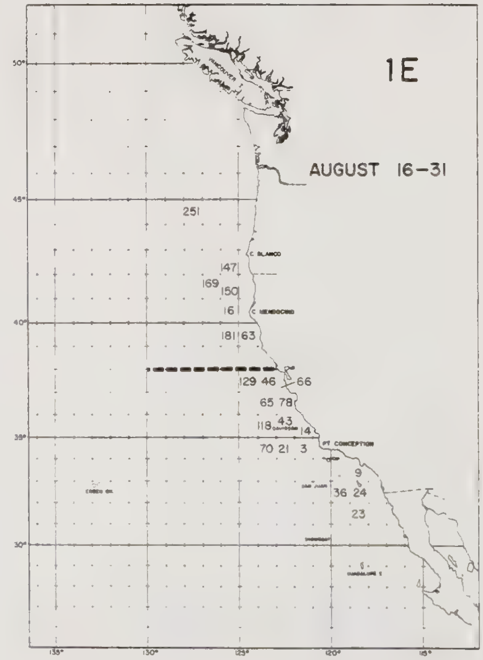
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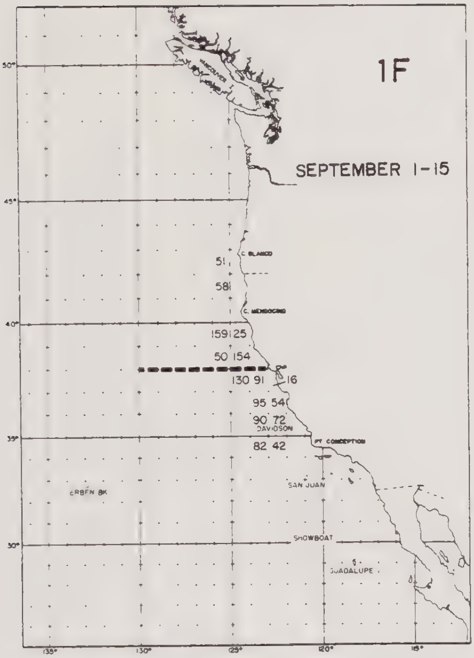
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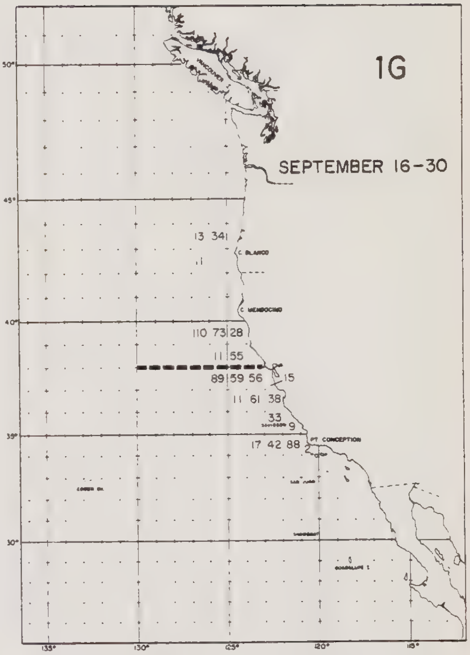
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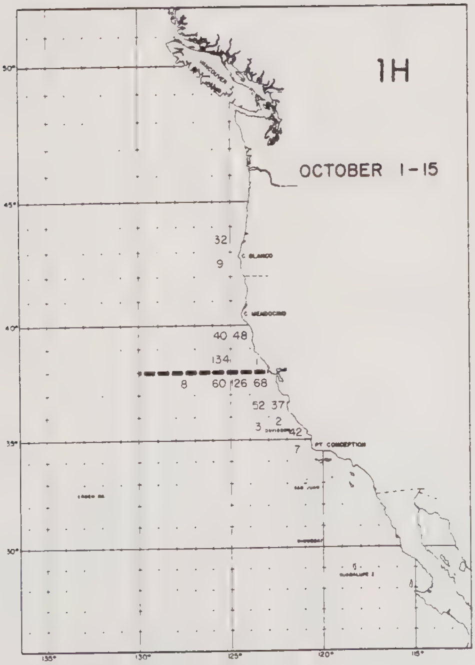
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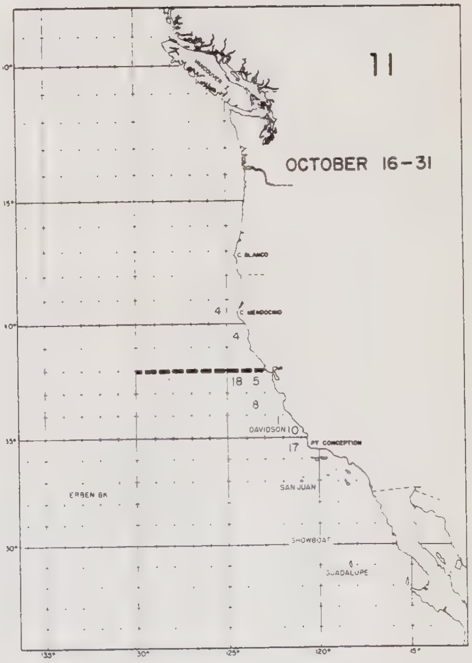
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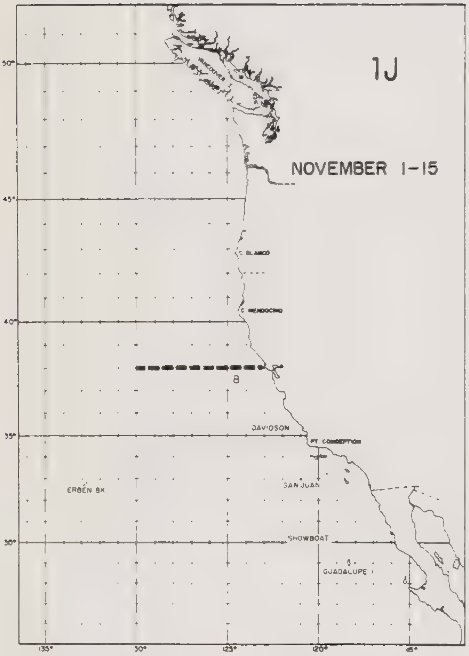
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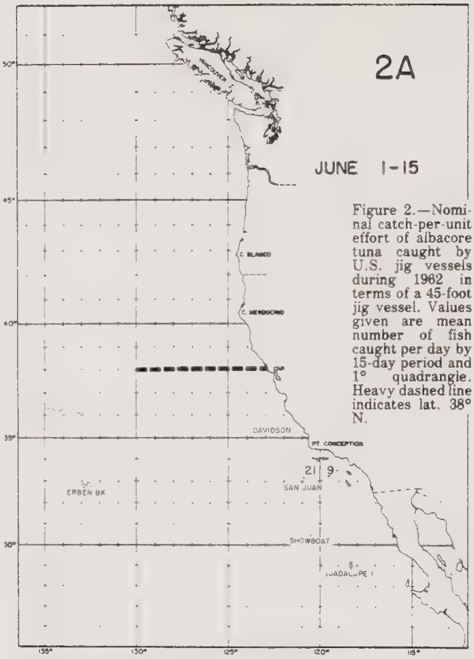
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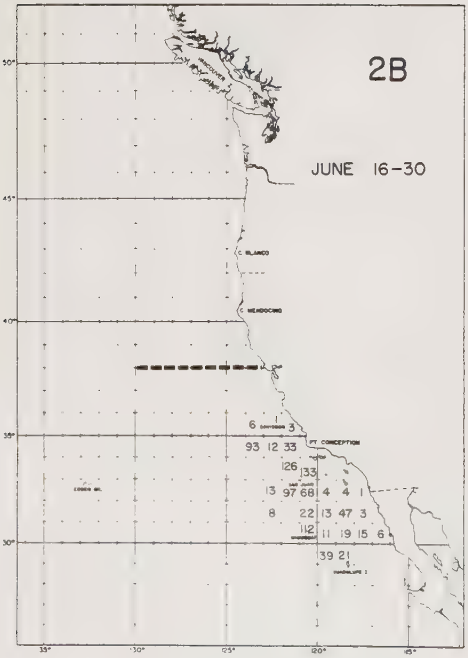
Figure 2.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1962 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.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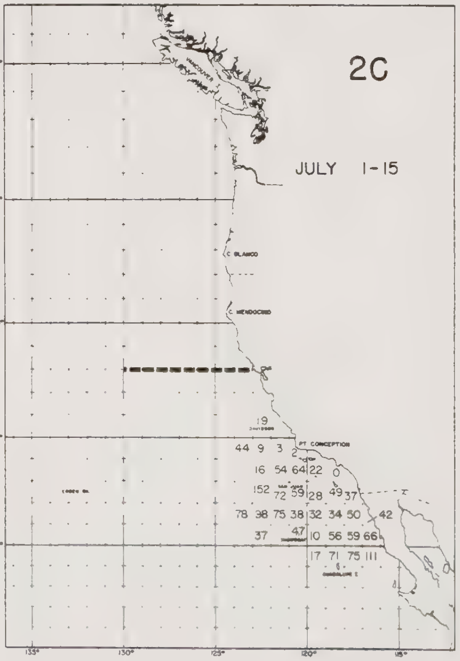
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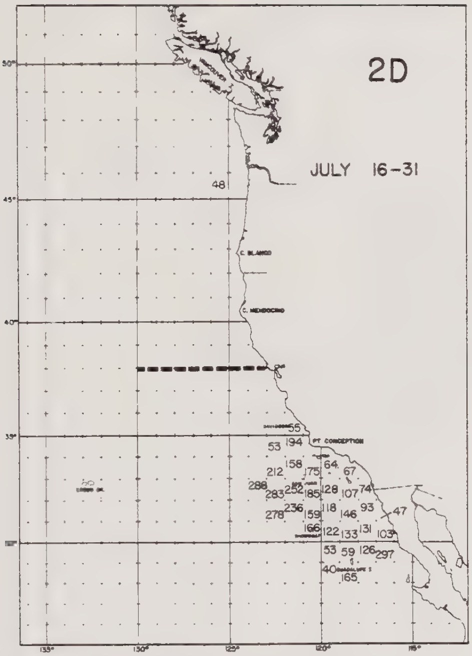
125°
120°
115°


2D
JULY 16-31
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT CONCEPTION
DAVIDSON
CORTES BK.
GUADALUPE I.
48
55
53 194
158 64 67
212 175
288 252 128 107 74
283 185
236 118 93
278 159 146 47
166 122 133 131 103
53 59 126 297
40
165
50°
45°
40°
35°
30°
135°
130°
125°
120°
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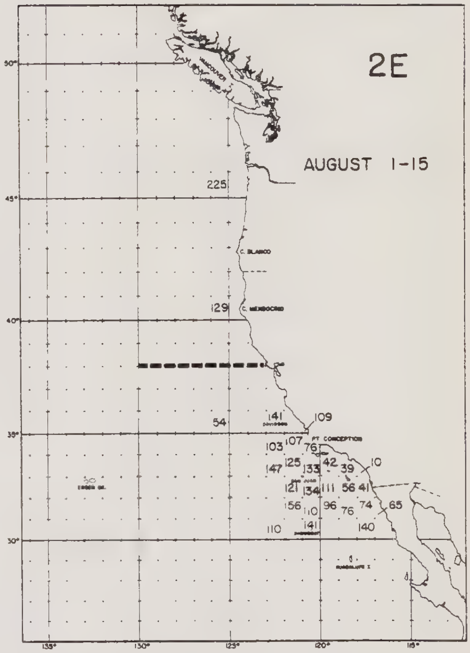
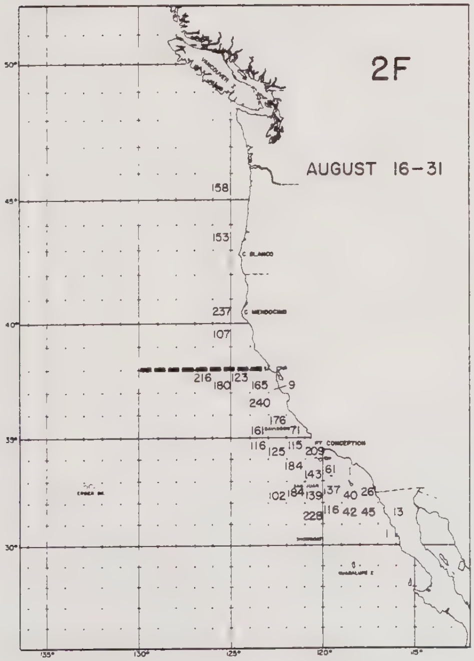
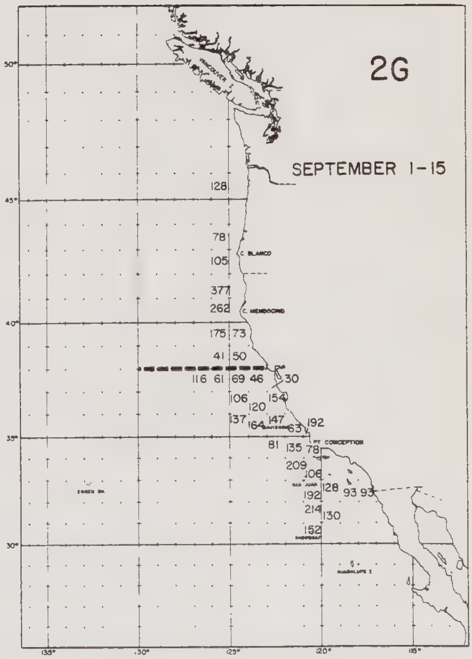
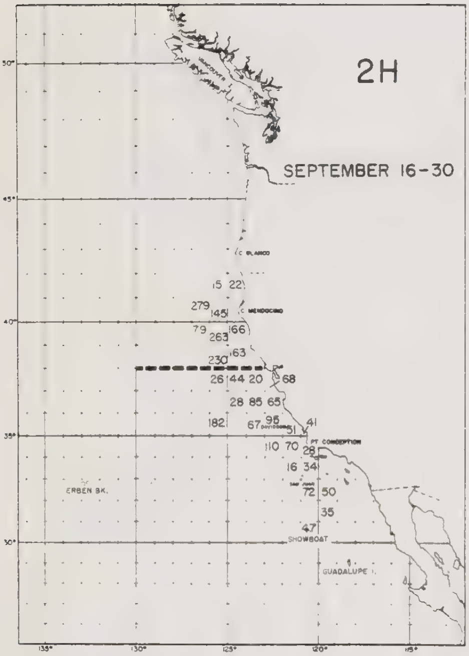

2E
AUGUST 1-15
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT CONCEPTION
DAVIDSON
CORTES BK.
GUADALUPE I.
225
129
141 109
54
103 107 76
125 42 39 10
147 133
121 134 111 56 41
156 110 96 76 74 65
110 141 140
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


2F
AUGUST 16-31
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT CONCEPTION
DAVIDSON
CORTES BK.
GUADALUPE I.
158
153
237
107
216 180 123 165 9
240
176
161 71
116 125 115 209
184
143 61
102 184 139 137 40 26
228 116 42 45 13
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


2G
SEPTEMBER 1-15
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT CONCEPTION
DAVIDSON
CORTES BK.
GUADALUPE I.
128
78
105
377
262
175 73
41 50
116 61 69 46 30
106 154
120
137 164 147 63 192
81 135 78
209
106
192 128 93 93
214 130
152
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°



2H

SEPTEMBER 16-30

C BLANCO
MENDOCINO
PT CONCEPTION
DAVIDSON
ERBEN BK.
SHOWBOAT
GUADALUPE I.
15 22
279 145
79 263 166
163
230
26 44 20 68
28 85 65
182 67 96 41
51
110 70 28
16 34
72 50
35
47
50°
45°
40°
35°
30°
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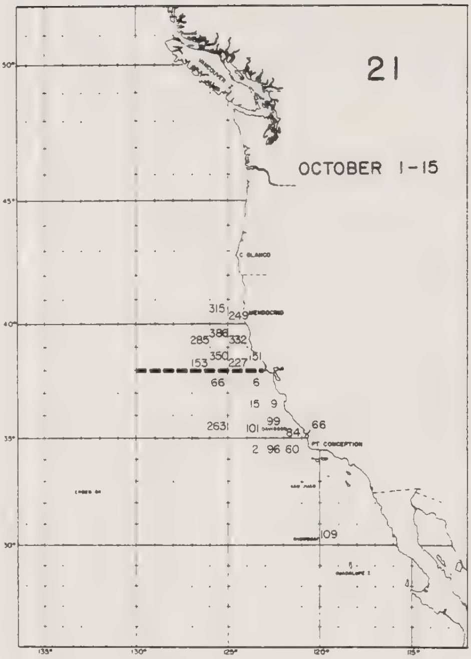
130°
125°
120°
115°



2I

OCTOBER 1-15

C BLANCO
MENDOCINO
PT CONCEPTION
315 249
285 388 332
350 227 151
153
66 6
15 9
263 101 99 66
84
2 96 60
109
50°
45°
40°
35°
30°
135°
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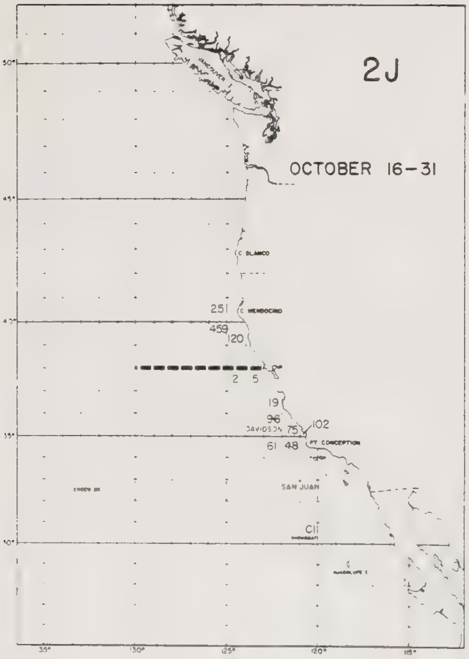
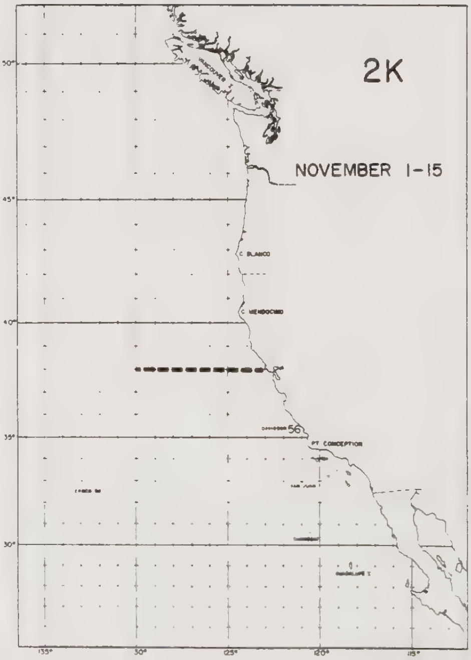
125°
120°
115°



2J

OCTOBER 16-31

C BLANCO
MENDOCINO
PT CONCEPTION
DAVIDSON
SAN JUAN
SHOWBOAT
251
459
120
2 5
19
96 102
75
61 48
C11
50°
45°
40°
35°
30°
35°
130°
125°
120°
115°



2K

NOVEMBER 1-15

C BLANCO
MENDOCINO
PT CONCEPTION
56
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45°
40°
35°
30°
135°
130°
125°
120°
115°

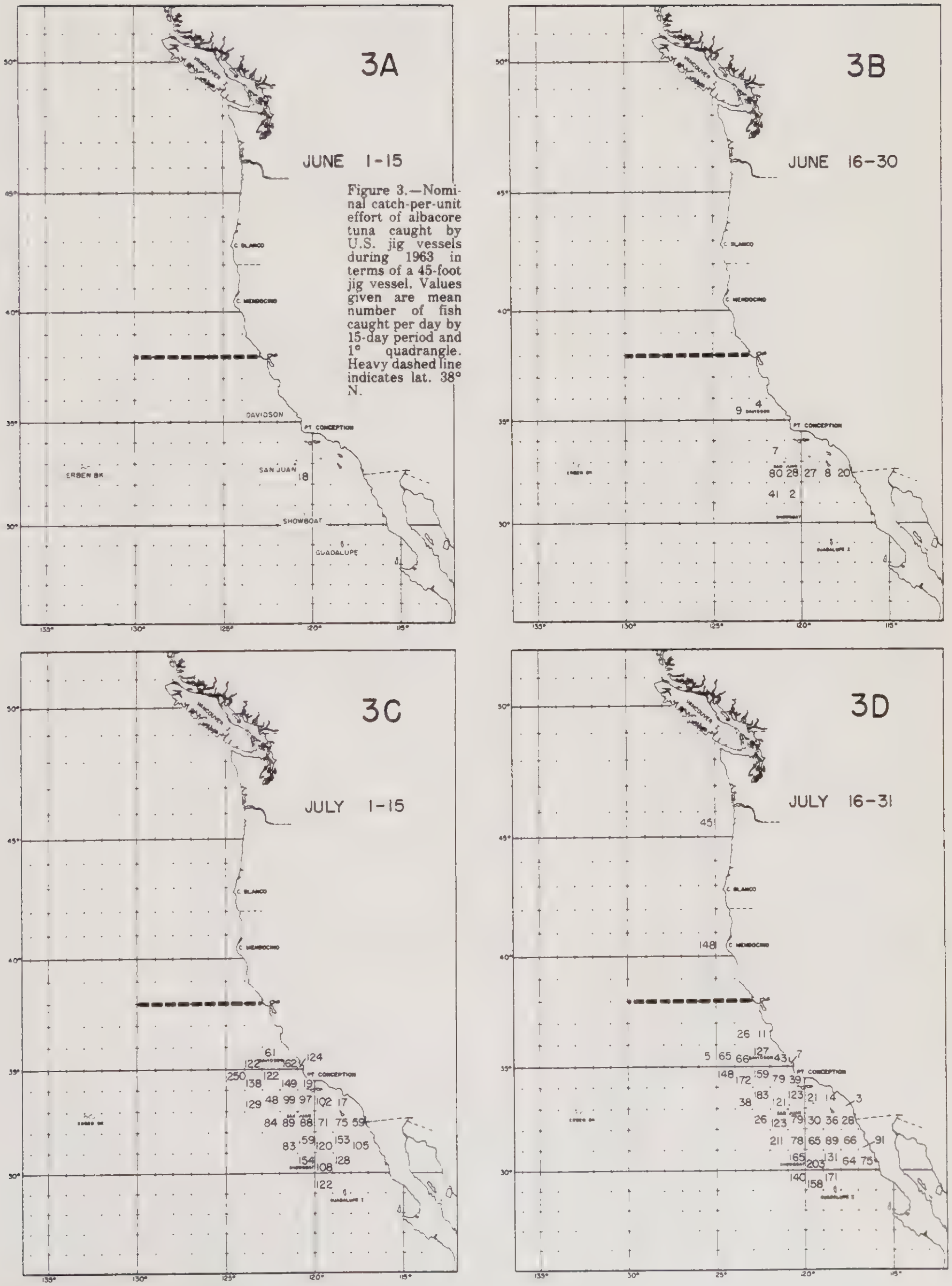
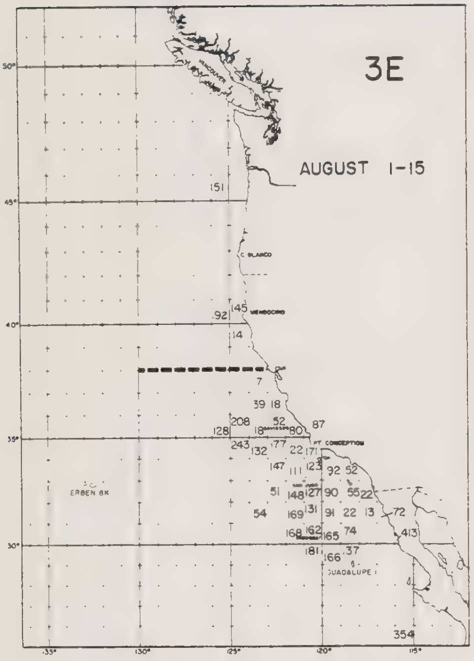

3A
JUNE 1-15
C BLANCO
C MENDOCINO
DAVIDSON
PT CONCEPTION
ERBEN BK
SAN JUAN
18
SHOWBOAT
GUADALUPE
3B
JUNE 16-30
4
9
7
80 28 27 8 20
41 2
3C
JULY 1-15
61
122 162 124
250 138 122 149 19
129 48 99 97 102 17
84 89 88 71 75 59
83 59 120 153 105
154 108 128
122
3D
JULY 16-31
45
148
26 11
5 65 66 127 43 7
148 172 159 79 39
38 183 121 123 21 14 3
26 123 79 30 36 28
211 78 65 89 66 91
165 203 131 64 75
140 158 171
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

Figure 3.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1963 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.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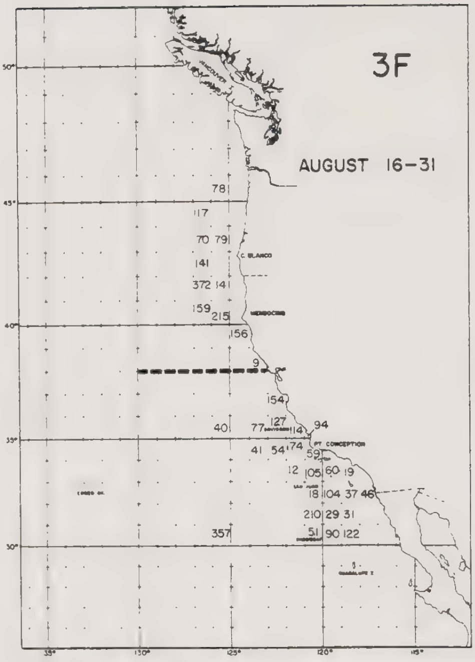
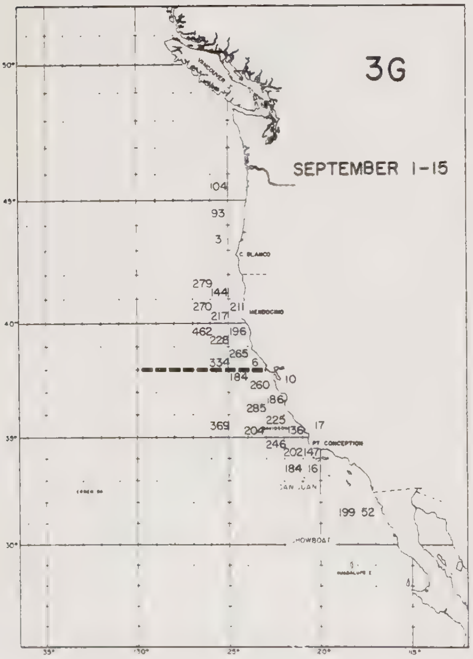
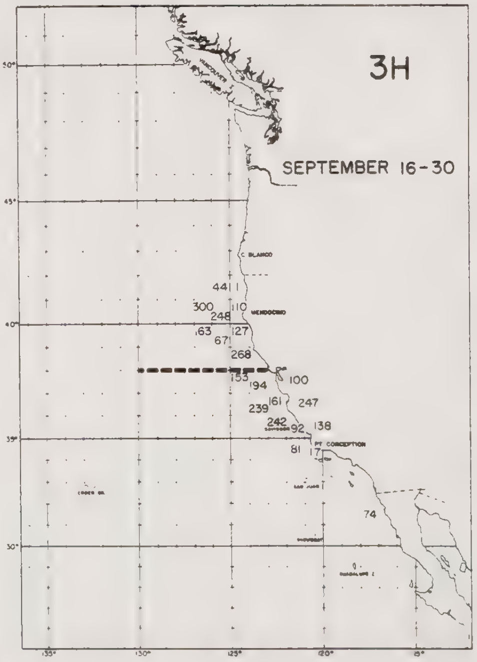
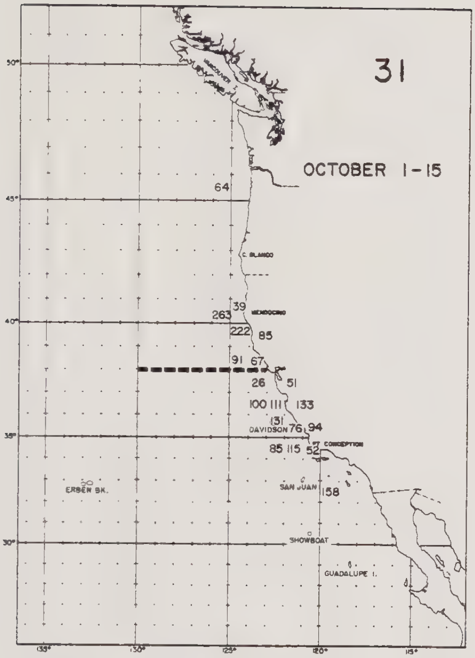
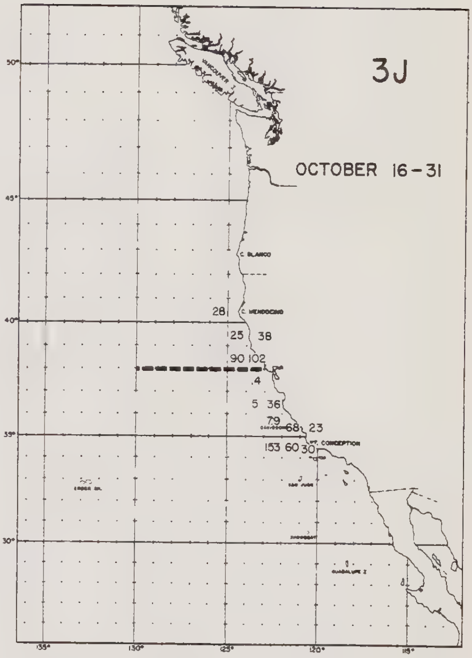
AUGUST 1-15
VANCOUVER
C. BLANCO
MENDOCINO
PT. CONCEPTION
ERBEN BK
GUADALUPE I

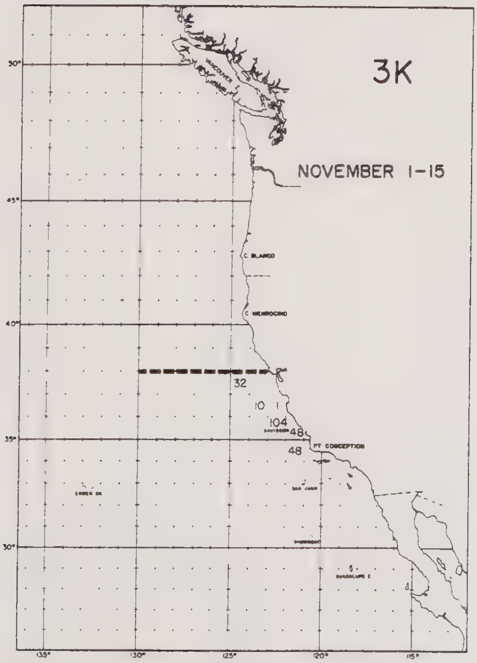

3F
AUGUST 16-31
C. BLANCO
MENDOCINO
PT. CONCEPTION

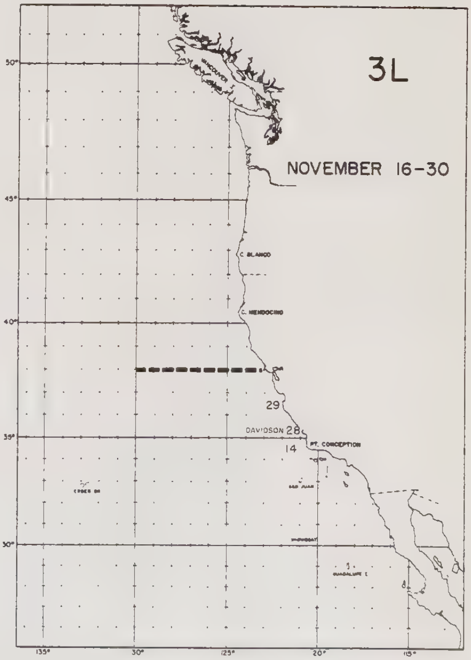

3G
SEPTEMBER 1-15
C. BLANCO
MENDOCINO
PT. CONCEPTION
SAN JUAN
SHOWBOAT


3H
SEPTEMBER 16-30
C. BLANCO
MENDOCINO
PT. CONCEPTION


3I
OCTOBER 1-15
VANCOUVER
C. BLANCO
MENDOCINO
PT. CONCEPTION
DAVIDSON
SAN JUAN
SHOWBOAT
GUADALUPE I.
ERBEN BK.
64
39
263
222
85
91
67
26
51
100
111
133
131
76
94
85
115
52
158
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


3J
OCTOBER 16-31
VANCOUVER
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
ERBEN BK.
28
25
38
90
102
4
5
36
79
68
23
153
60
30
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


3K
NOVEMBER 1-15
VANCOUVER
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
ERBEN BK.
32
10
1
104
48
48
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


3L
NOVEMBER 16-30
VANCOUVER
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
DAVIDSON
ERBEN BK.
29
28
14
50°
45°
40°
35°
30°
135°
30°
125°
20°
115°

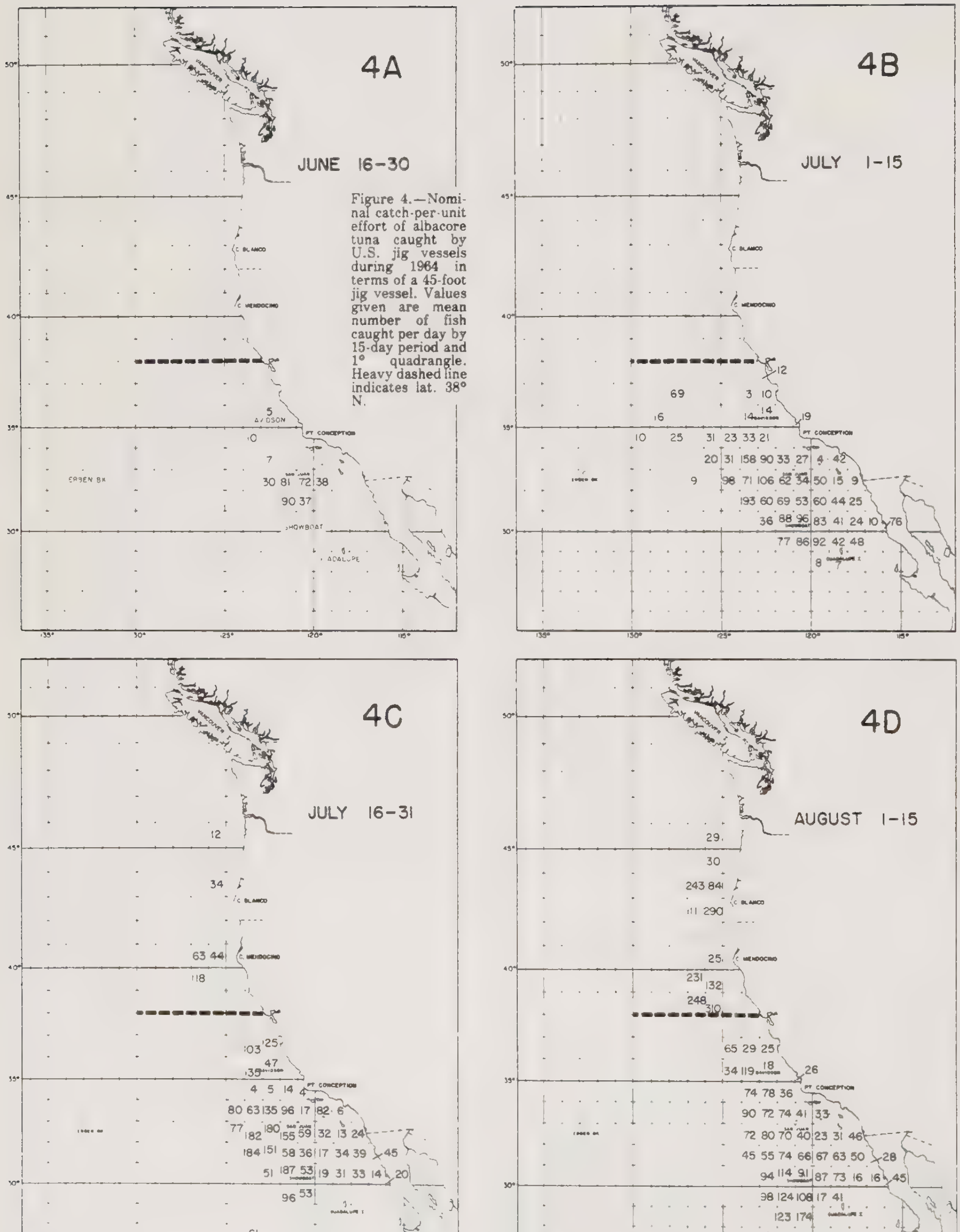
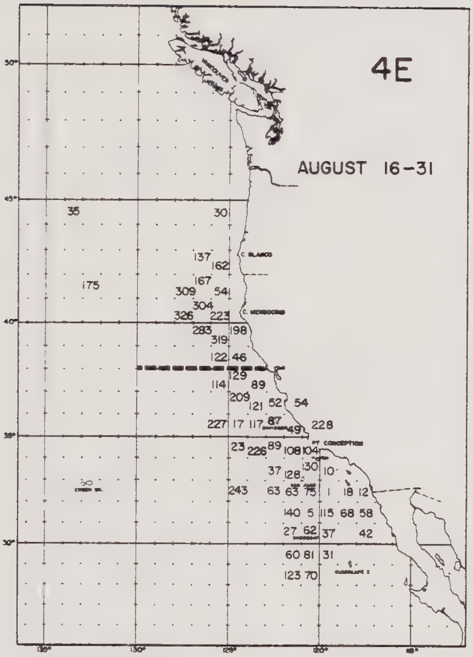
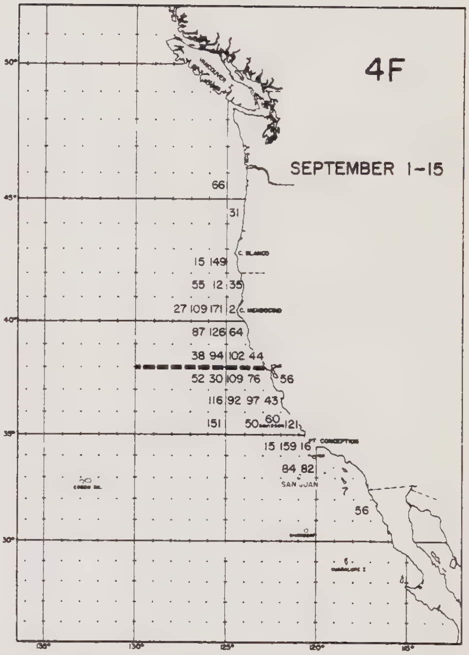
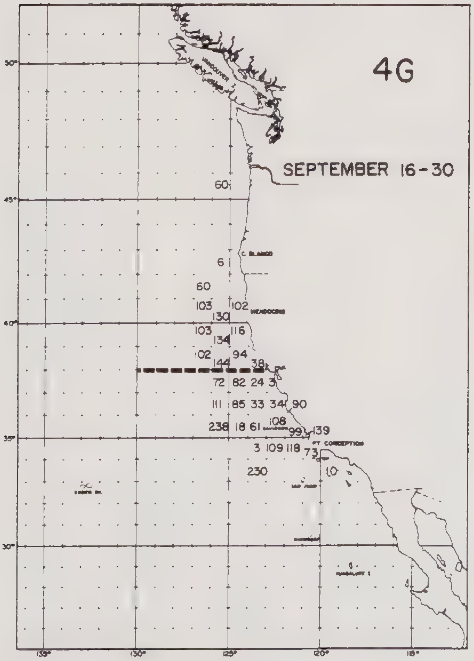
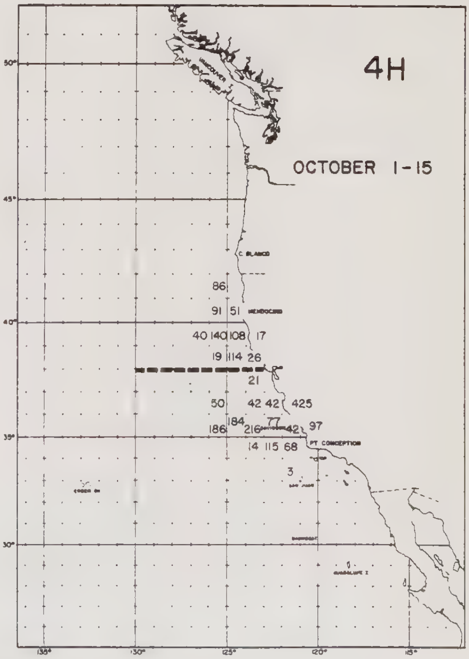

4A
JUNE 16-30
C. BLANCO
C. MENDOCINO
5
DAVIDSON
PT CONCEPTION
10
7
ERBEN BK
30 81 72 38
90 37
SHOWBOAT
GUADALUPE
4B
JULY 1-15
C. BLANCO
C. MENDOCINO
12
69
3 10
14
16
14
19
PT CONCEPTION
10 25 31 23 33 21
20 31 158 90 33 27 4 42
9
98 71 106 62 34 50 15 9
193 60 69 53 60 44 25
36 88 96 83 41 24 10 76
77 86 92 42 48
8
4C
JULY 16-31
12
34
C. BLANCO
63 44
C. MENDOCINO
118
103 125
47
135
4 5 14 4
PT CONCEPTION
80 63 135 96 17 82 6
77 182 180 155 59 32 13 24
184 151 58 36 17 34 39 45
51 187 53 19 31 33 14 20
96 53
61
4D
AUGUST 1-15
29
30
243 84
C. BLANCO
111 290
25
C. MENDOCINO
231
132
248
310
65 29 25
34 119 18
26
PT CONCEPTION
74 78 36
90 72 74 41 33
72 80 70 40 23 31 46
45 55 74 66 67 63 50 28
94 114 91 87 73 16 16 45
98 124 108 17 41
123 174
221
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

Figure 4.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1964 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.


4E
AUGUST 16-31
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
SAN JUAN
CORTES BK.
GUADALUPE I.
35 30
137 162
175 167
309 54
304
326 223
283 198
319
122 46
129
114 89
209
121 52 54
227 17 117 87 49 228
23 226 89 108 104
37 128 130 10
243 63 63 75 1 18 12
140 5 115 68 58
27 62 37 42
60 81 31
123 70
50° 45° 40° 35° 30°
135° 130° 125° 120° 115°


4F
SEPTEMBER 1-15
VANCOUVER I.
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
SAN JUAN
CORTES BK.
GUADALUPE I.
66
31
15 149
55 12 35
27 109 171 2
87 126 64
38 94 102 44
52 30 109 76 56
116 92 97 43
151 50 60 121
15 159 16
84 82
7
56
50° 45° 40° 35° 30°
135° 130° 125° 120° 115°


4G
SEPTEMBER 16-30
VANCOUVER I.
C. BLANCO
MENDOCINO
PT. CONCEPTION
SAN JUAN
CORTES BK.
GUADALUPE I.
60
6
60
103 102
130
103 116
134
102 94
144 38
72 82 24 3
111 85 33 34 90
238 18 61 108 99 139
3 109 118 73
230 10
50° 45° 40° 35° 30°
135° 130° 125° 120° 115°


4H
OCTOBER 1-15
VANCOUVER I.
C. BLANCO
MENDOCINO
PT. CONCEPTION
SAN JUAN
CORTES BK.
GUADALUPE I.
86
91 51
40 140 108 17
19 114 26
21
50 42 42 425
186 184 216 77 42 97
14 115 68
3
50° 45° 40° 35° 30°
135° 130° 125° 120° 115°

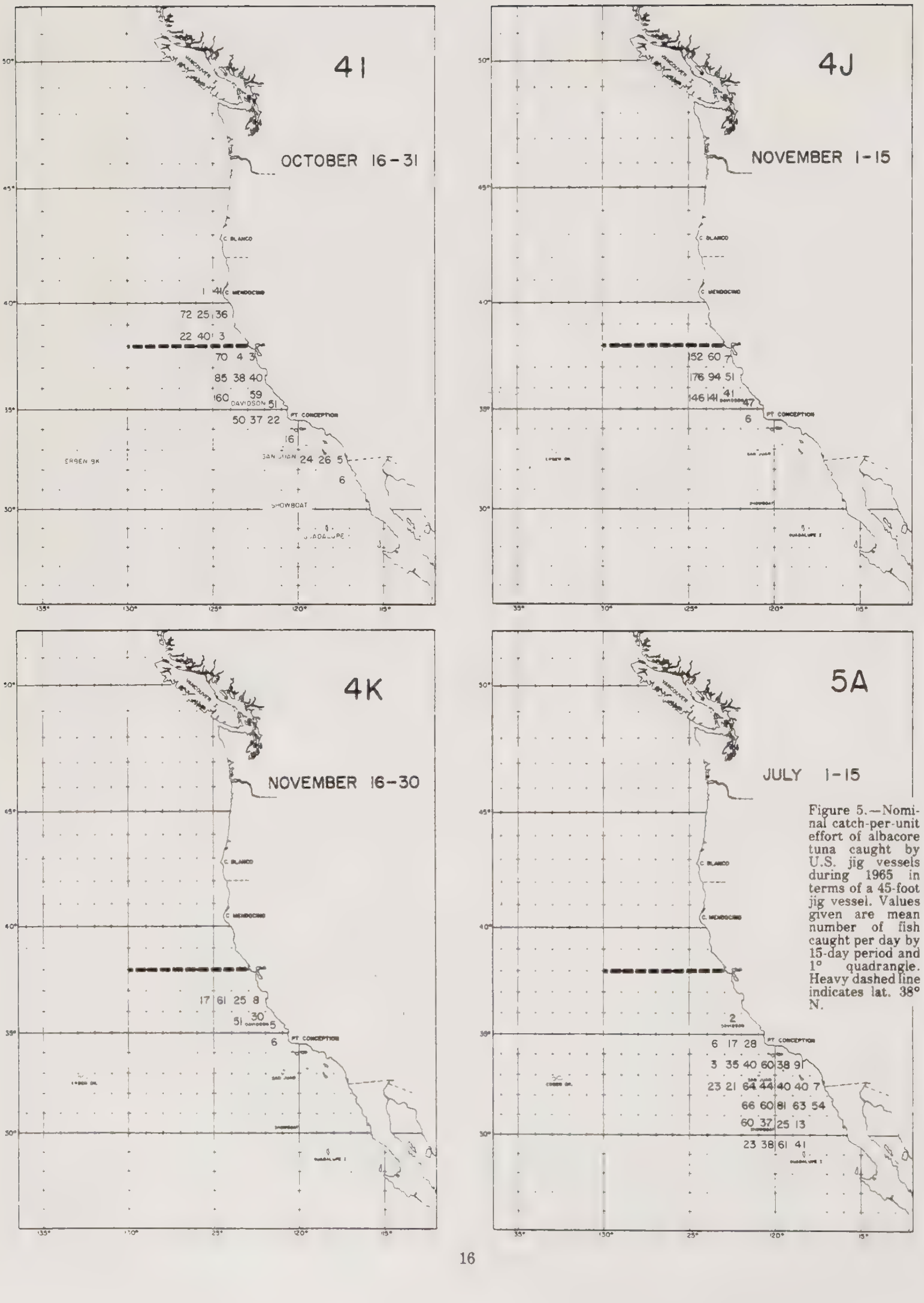
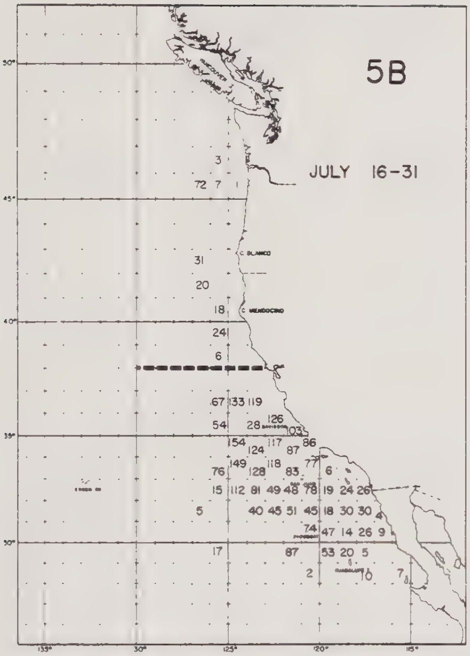

4I
OCTOBER 16-31
C. BLANCO
C. MENDOCINO
PT CONCEPTION
DAVIDSON
SAN JUAN
SHOWBOAT
GUADALUPE
1 41
72 25 36
22 40 3
70 4 3
85 38 40
160 59 51
50 37 22
16
24 26 5
6
4J
NOVEMBER 1-15
152 60 7
176 94 51
146 141 41 47
6
4K
NOVEMBER 16-30
17 61 25 8
51 30 5
6
5A
JULY 1-15
2
6 17 28
3 35 40 60 38 9
23 21 64 44 40 40 7
66 60 81 63 54
60 37 25 13
23 38 61 41
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

Figure 5.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1965 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.


5B
JULY 16-31
VANCOUVER
C. BLANCO
C. MENDOCINO
SAN JUAN
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
3
72 7 1
31
20
18
24
6
67 133 119
54 28 126
103
154 124 117 87 86
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76 128 83 6
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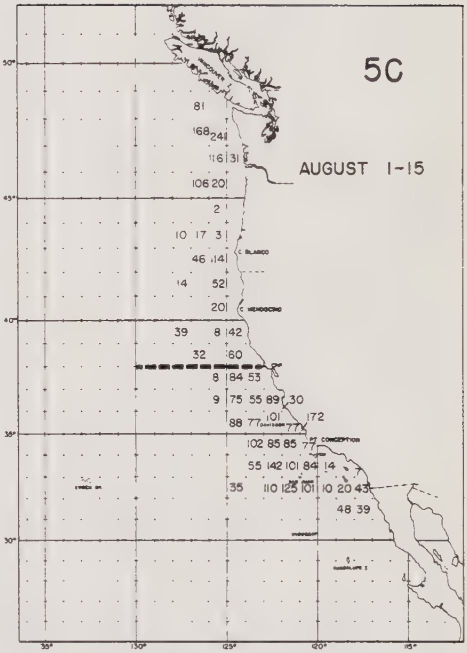
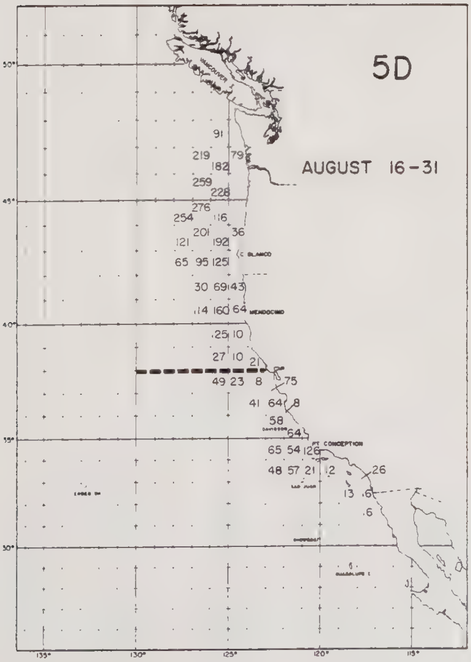
5 40 45 51 45 18 30 30 4
74 47 14 26 9
17 87 53 20 5
2 10 7


5C
AUGUST 1-15
VANCOUVER
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
GUADALUPE I.
50°
45°
40°
35°
30°
35°
130°
125°
120°
115°
81
168 241
116 31
106 201
2
10 17 3
46 141
14 521
201
39 8 142
32 60
8 184 53
9 175 55 89 30
88 77 101 77 172
102 85 85 77
55 142 101 84 14
35 110 125 101 10 20 43
48 39


5D
AUGUST 16-31
VANCOUVER
C. BLANCO
MENDOCINO
PT. CONCEPTION
SAN JUAN
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
91
219 79
182
259
228
276
254 116
201 36
121 192
65 95 125
30 69 143
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125 10
27 10 21
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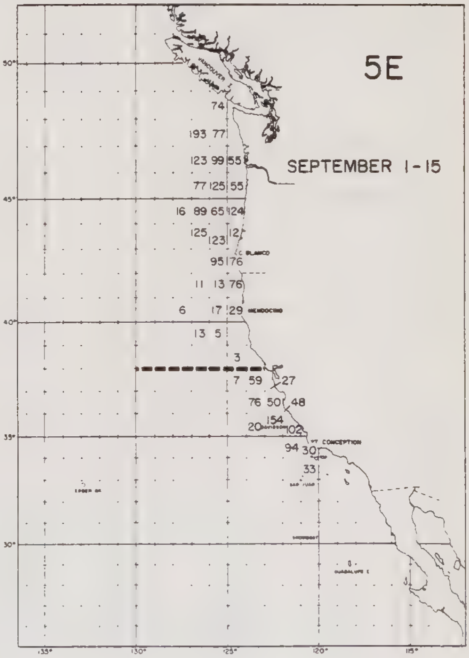
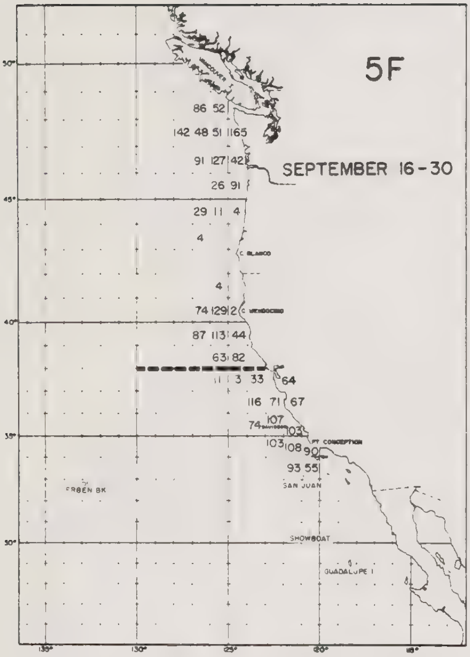
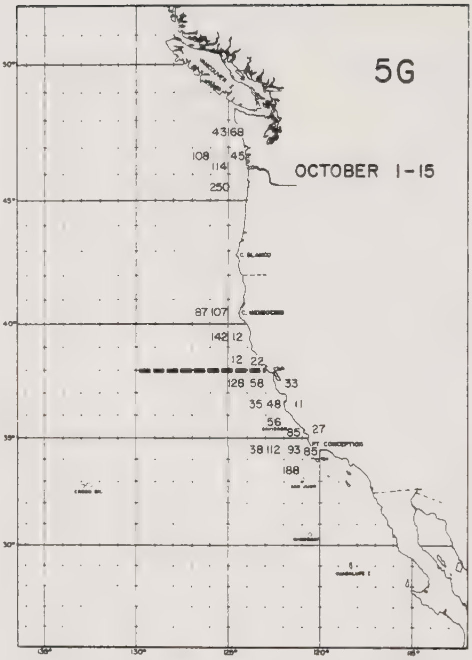
41 64 8
58
64
65 54 126
48 57 21 12 26
13 6
6


5E
SEPTEMBER 1-15
VANCOUVER
C. BLANCO
MENDOCINO
PT. CONCEPTION
SAN JUAN
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
74
193 77
123 99 55
77 125 55
16 89 65 124
125 123 12
95 176
11 13 76
6 17 129
13 5
3
7 59 27
76 50 48
20 154 102
94 30
33


5F
SEPTEMBER 16-30
86 52
142 48 51 1165
91 127 42
26 91
29 11 4
4
C. BLANCO
4
74 129 2
C. MENDOCINO
87 113 44
63 82
11 3 33
64
116 71 67
74 107
103
103 108 90
PT CONCEPTION
93 55
SAN JUAN
CORTES BK
SHOWBOAT
GUADALUPE I
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


5G
OCTOBER 1-15
43 168
108 45
114
250
C. BLANCO
87 107
C. MENDOCINO
142 12
12 22
128 58
33
35 48 11
56
85 27
PT CONCEPTION
38 112 93 85
188
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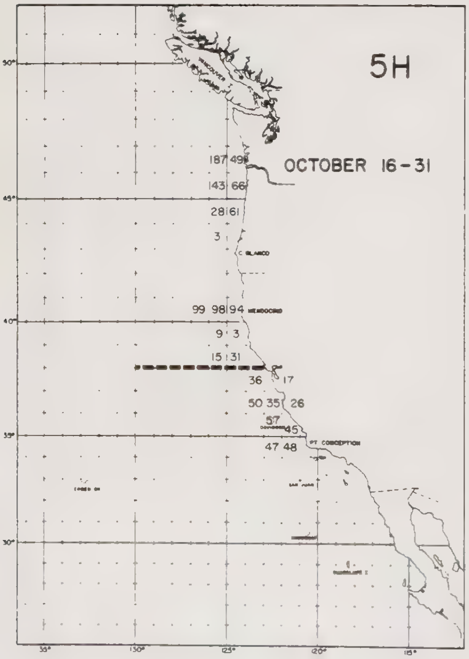
45°
40°
35°
30°
130°
125°
120°
115°


5H
OCTOBER 16-31
187 49
143 66
28 61
3
C. BLANCO
99 98 94
MENDOCINO
9 3
15 31
36 17
50 35 26
57
45
PT CONCEPTION
47 48
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45°
40°
35°
30°
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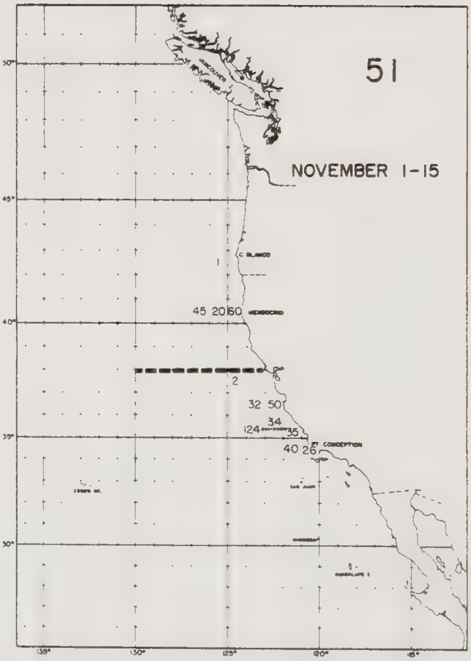
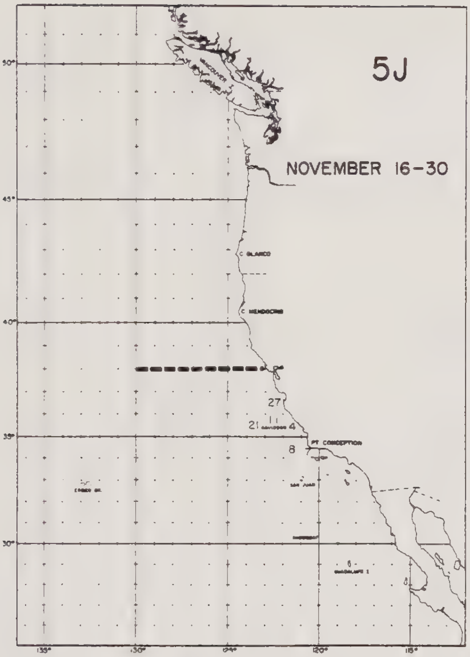
130°
125°
120°
115°


5I
NOVEMBER 1-15
C. BLANCO
1
45 20 60
MENDOCINO
2
32 50
34
124 35
PT CONCEPTION
40 26
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


5J
NOVEMBER 16–30
50°
45°
40°
35°
30°
C BLANCO
C MENDOCINO
PT CONCEPTION
27
21
11
4
8
7
135°
130°
125°
120°
115°

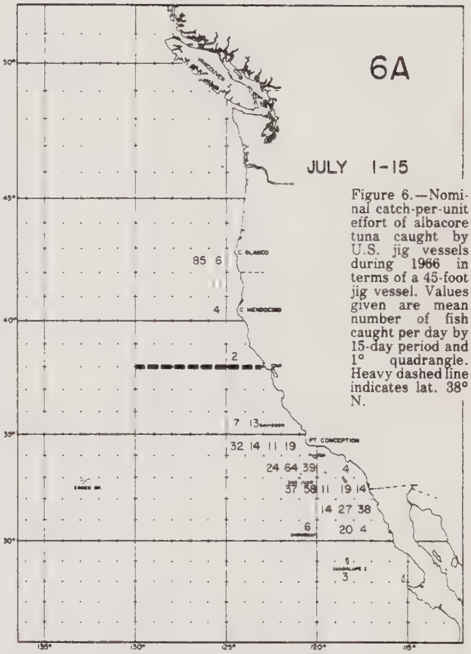
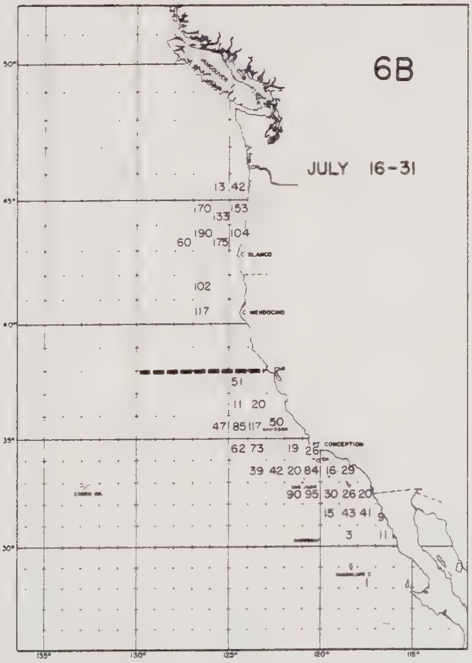
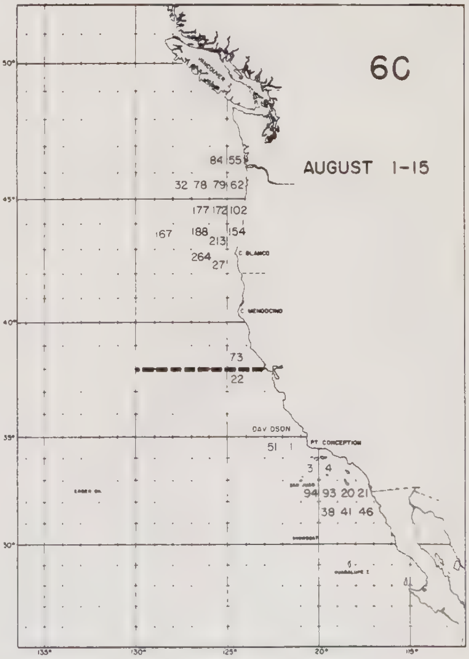
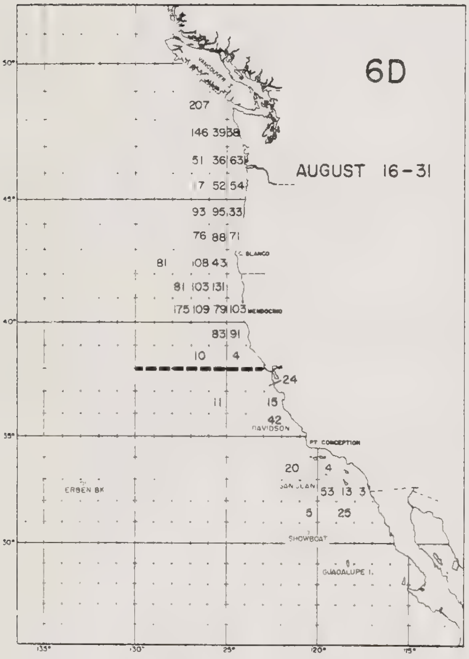
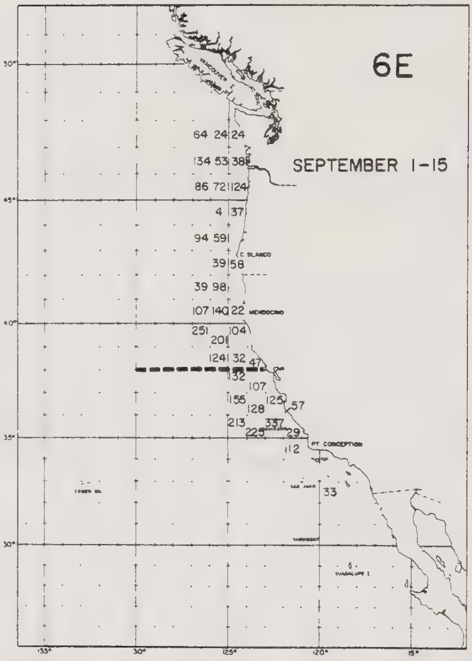

6A
JULY 1–15
85 6
4
2
7 13
PT CONCEPTION
32 14 11 19
24 64 39 4
37 58 11 19 14
14 27 38
6 20 4
3
C BLANCO
C MENDOCINO
135°
130°
125°
120°
115°

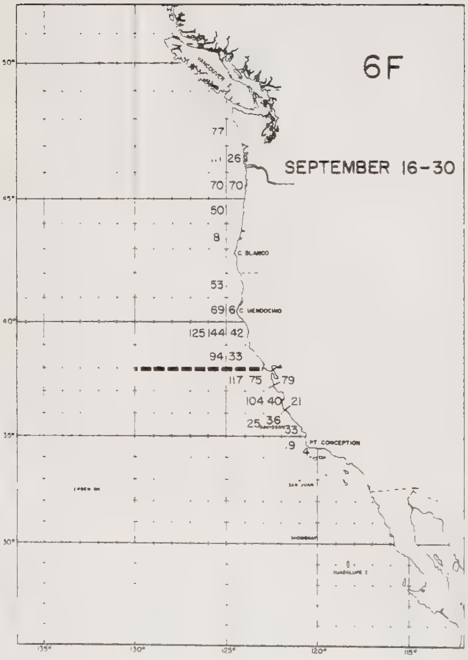
Figure 6.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1966 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.

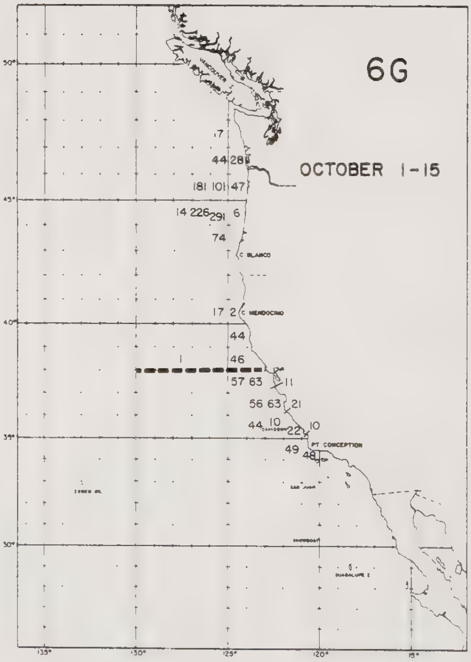

6B
JULY 16–31
13 42
170 133 153
190 175 104
60
102
117
51
11 20
47 85 117 50
62 73 19 26
39 42 20 84 16 29
90 95 30 26 20
15 43 41 9
3 11
1
C BLANCO
C MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


6C
AUGUST 1–15
84 55
32 78 79 62
177 172 102
167 188 154
213
264 27
73
22
DAVIDSON
51 1
3 4
94 93 20 21
38 41 46
C BLANCO
C MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


6D
AUGUST 16-31
VANCOUVER I.
207
146 39 38
51 36 63
17 52 54
93 95 33
76 88 71
C. BLANCO
81 108 43
81 103 131
175 109 79 103
MENDOCINO
83 91
10 4
24
11 15
42
DAVIDSON
PT CONCEPTION
20 4
SAN JUAN
53 13 3
5 25
SHOWBOAT
ERBEN BK
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


6E
SEPTEMBER 1-15
VANCOUVER I.
64 24 24
134 53 38
86 72 124
4 37
94 59
C. BLANCO
39 58
39 98
107 140 22
MENDOCINO
251 104
201
124 32 47
132
107
155 125 57
128
213 337
225 29
DAVIDSON
PT CONCEPTION
112
SAN JUAN
33
SHOWBOAT
ERBEN BK
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


6F
SEPTEMBER 16-30
VANCOUVER I.
77
26
70 70
50
8
C. BLANCO
53
69 6
C. MENDOCINO
125 144 42
94 33
117 75 79
104 40 21
25 36
DAVIDSON
33
PT CONCEPTION
9
4
SAN JUAN
SHOWBOAT
ERBEN BK
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


6G
OCTOBER 1-15
VANCOUVER I.
17
44 28
181 101 47
14 226 291 6
74
C. BLANCO
17 2
C. MENDOCINO
44
1 46
57 63 11
56 63 21
44 10 22 10
DAVIDSON
PT CONCEPTION
49 48
SAN JUAN
SHOWBOAT
ERBEN BK
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

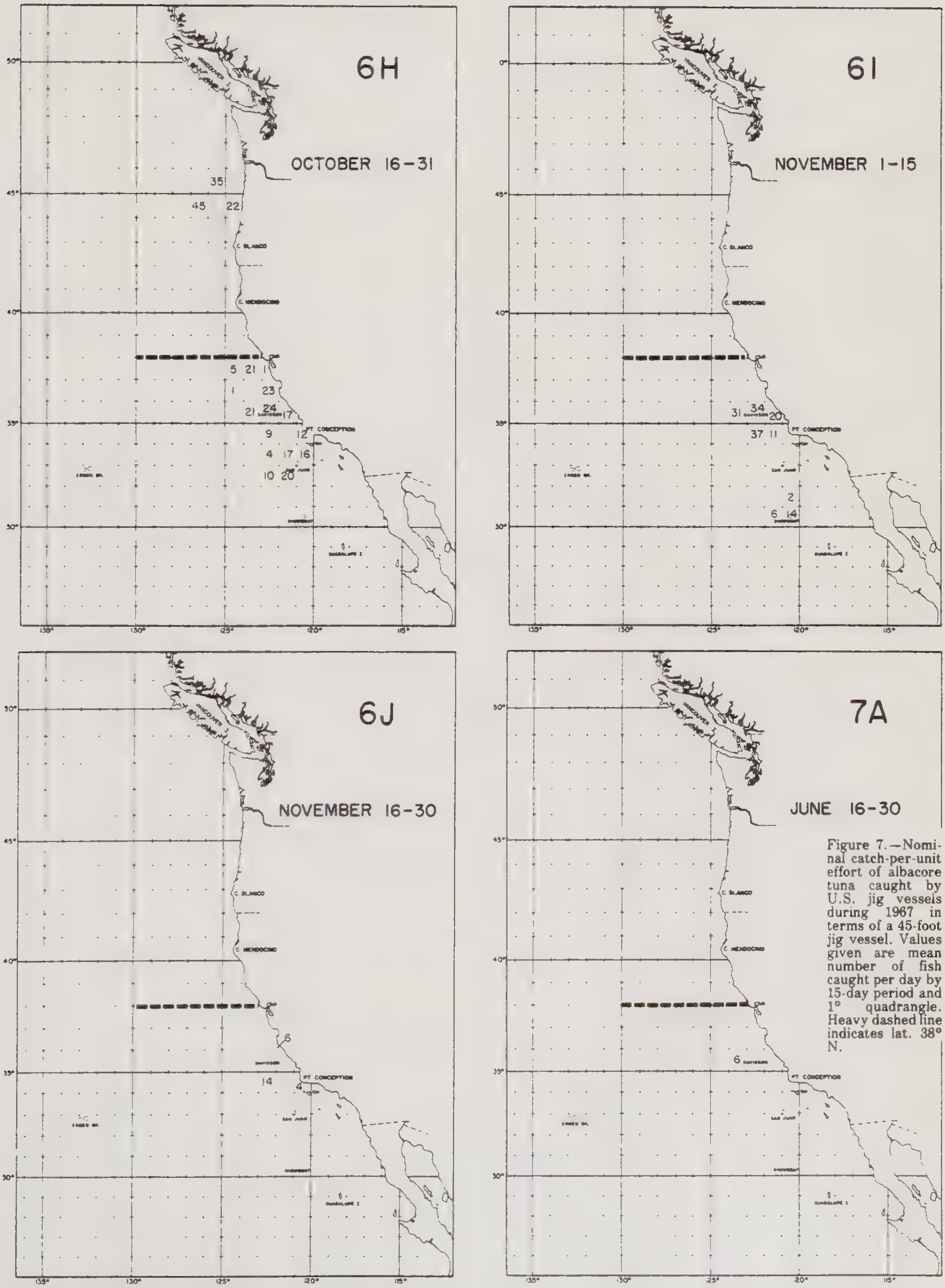
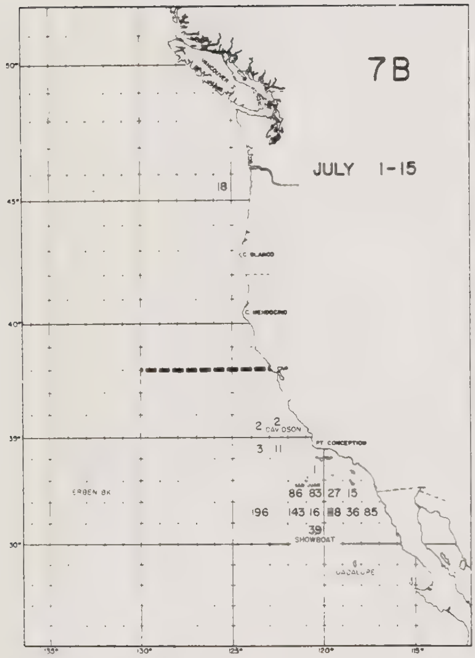
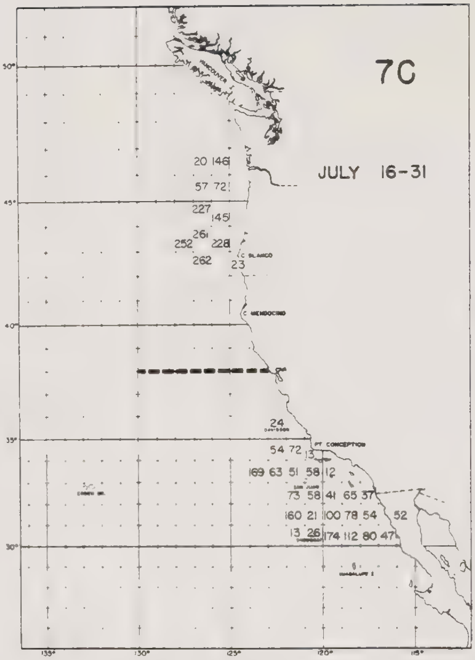
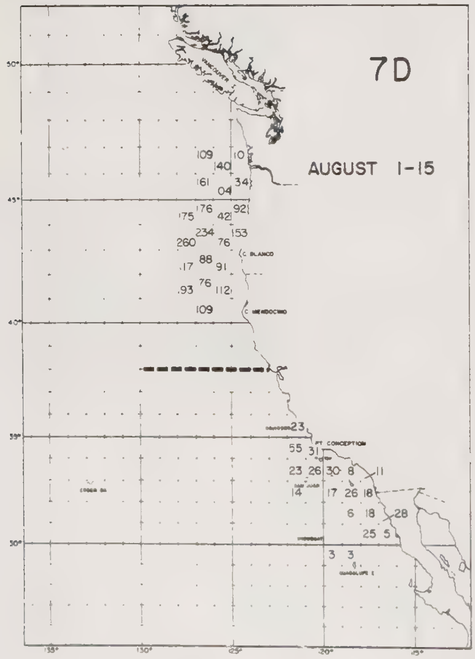
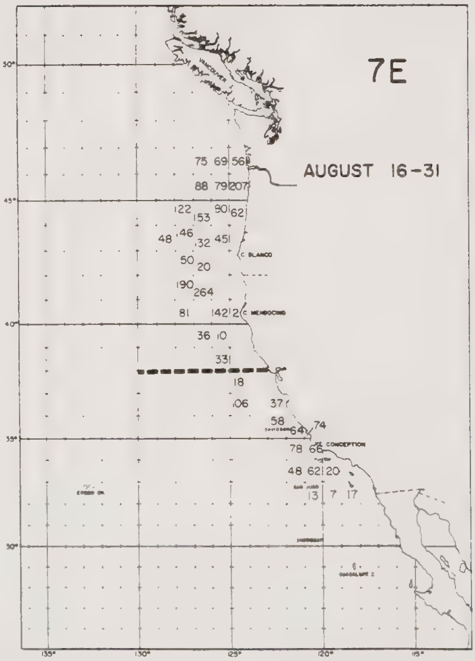

6H
OCTOBER 16-31
35
45 22
5 21 1
1 23
21 24 17
9 12
4 17 16
10 20
6I
NOVEMBER 1-15
31 34 20
37 11
2
6 14
6J
NOVEMBER 16-30
6
14
4
7A
JUNE 16-30
6
C. BLANCO
C. MENDOCINO
PT CONCEPTION
SAN JUAN
GUADALUPE I
VANCOUVER
COBB SM.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

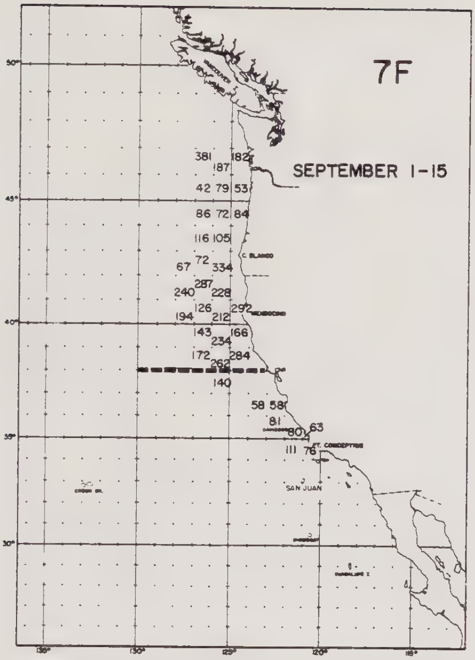
Figure 7.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1967 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.


7B
JULY 1-15
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
VANCOUVER
18
C BLANCO
C MENDOCINO
2 2
DAVIDSON
PT CONCEPTION
3 11
1
SAN JUAN
86 83 27 15
ERBEN BK
196
143 16 8 36 85
39
SHOWBOAT
GUADALUPE


7C
JULY 16-31
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
VANCOUVER
20 146
57 72
227
145
261
252 228
262 23
C BLANCO
C MENDOCINO
24
DAVIDSON
PT CONCEPTION
54 72 13
169 63 51 58 12
SAN JUAN
73 58 41 65 37
160 21 100 78 54 52
13 26 174 112 80 47
SHOWBOAT
ERBEN BK
GUADALUPE I


7D
AUGUST 1-15
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
VANCOUVER
109 10
140
161 34
04
175 176 42 92
234 153
260 76
C BLANCO
17 88 91
93 76 112
109
C MENDOCINO
DAVIDSON 23
PT CONCEPTION
55 31
23 26 30 8 11
SAN JUAN
14 17 26 18
6 18 28
25 5
SHOWBOAT
3 3
GUADALUPE I
ERBEN BK

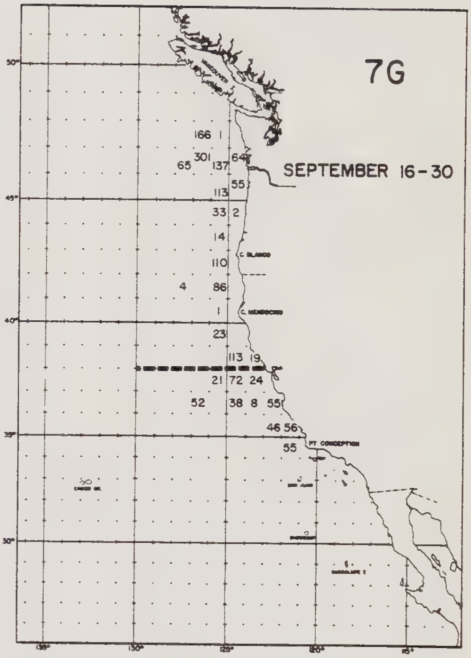

7E
AUGUST 16-31
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
VANCOUVER
75 69 56
88 79 207
122 80 62
153
48 46 32 451
C BLANCO
50 20
190 264
81 142 12
C MENDOCINO
36 10
331
18
106 37
58
DAVIDSON 64 74
PT CONCEPTION
78 66
48 62 120
SAN JUAN
13 7 17
SHOWBOAT
GUADALUPE I
ERBEN BK



7F

SEPTEMBER 1-15

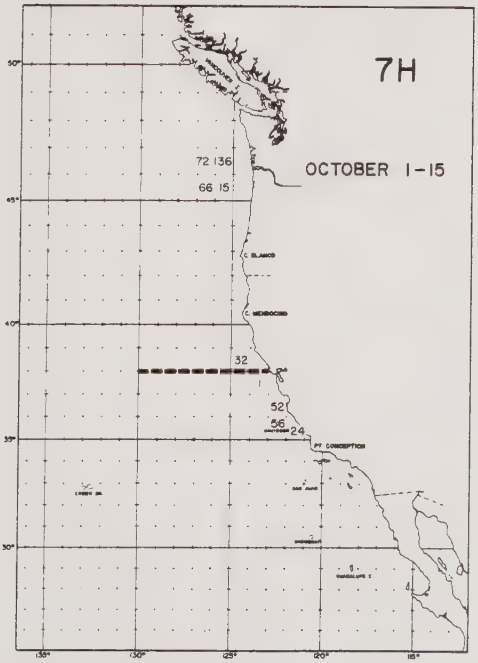
381 182
187
42 79 53
86 72 84
116 105
C. BLANCO
67 72 334
287
240 228
126 292
194 212
MENDOCINO
143 166
234
172 284
262
140
58 58
81
80 63
111 76
PT. CONCEPTION
SAN JUAN
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°



7G

SEPTEMBER 16-30

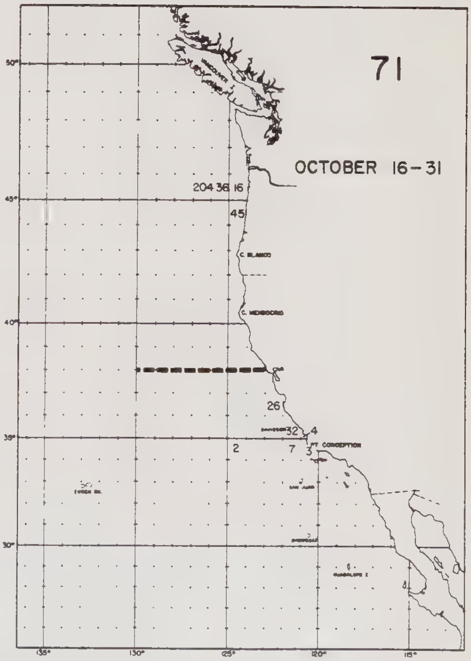
166 1
301 64
65 137
55
113
33 2
14
C. BLANCO
110
4 86
1 C. MENDOCINO
23
113 19
21 72 24
52 38 8 55
46 56
55
PT. CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°



7H

OCTOBER 1-15

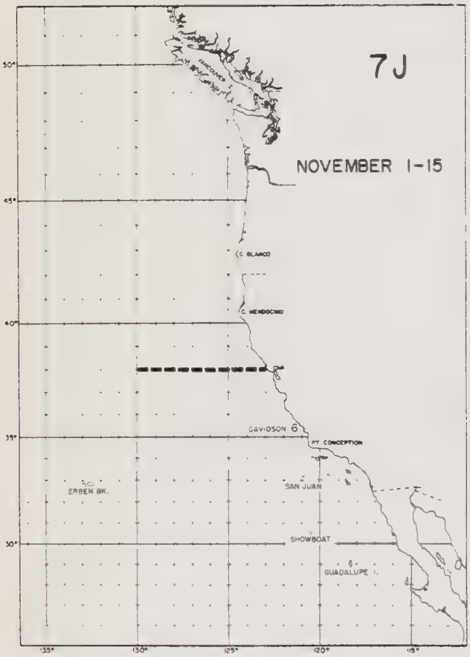
72 136
66 15
C. BLANCO
C. MENDOCINO
32
52
56
24
PT. CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°



7I

OCTOBER 16-31

204 36 16
45
C. BLANCO
C. MENDOCINO
26
32 4
2 7 3
PT. CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


7J
NOVEMBER 1-15
VANCOUVER ISLAND
C. BLANCO
C. MENDOCINO
DAVIDSON 6
PT CONCEPTION
SAN JUAN
ERBEN BK.
SHOWBOAT
GUADALUPE I.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

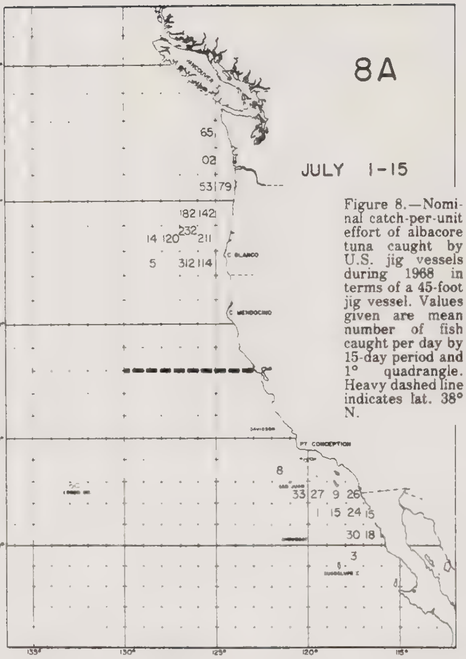
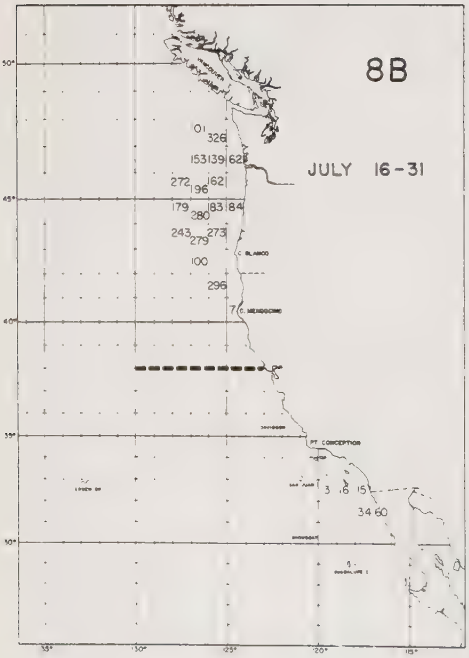
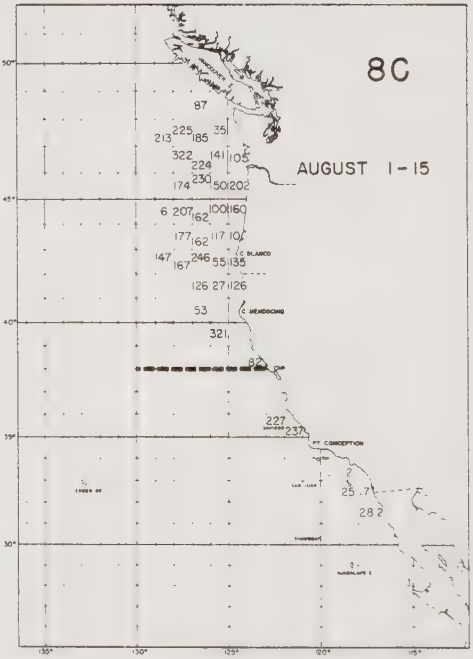
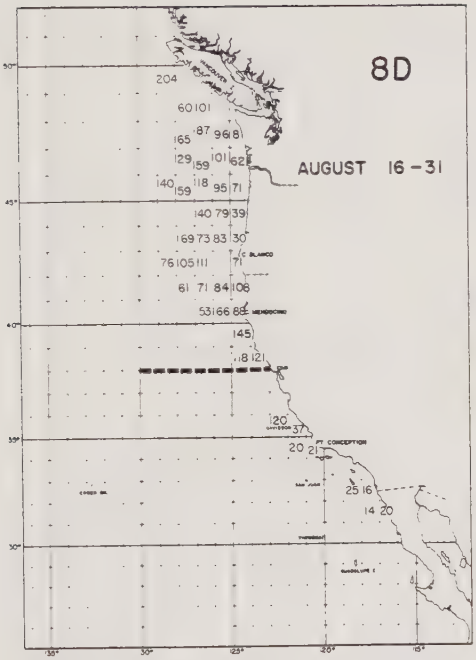
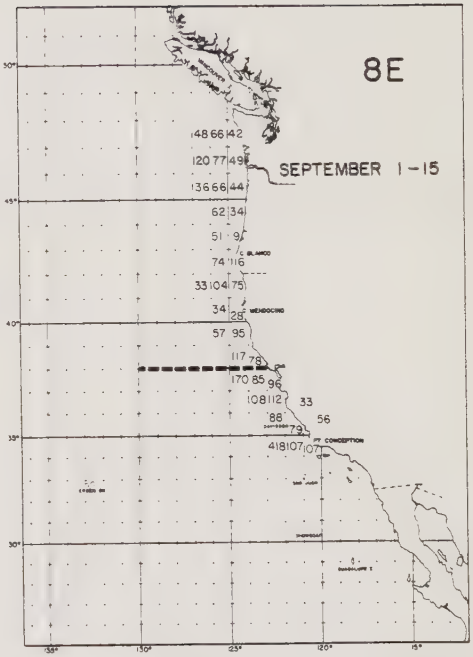

8A
JULY 1-15
VANCOUVER ISLAND
65
02
53 79
182 142
232
14 120 211
5 312 114
C. BLANCO
C. MENDOCINO
DAVIDSON
PT CONCEPTION
8
SAN JUAN
33 27 9 26
1 15 24 15
30 18
SHOWBOAT
3
GUADALUPE I.
ERBEN BK.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

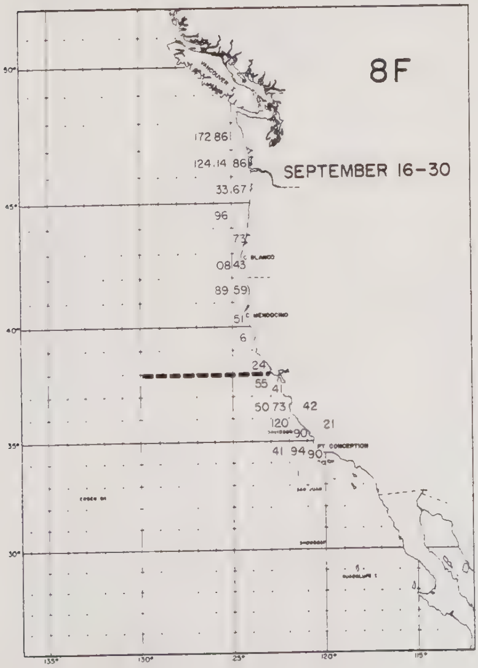
Figure 8.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1968 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.

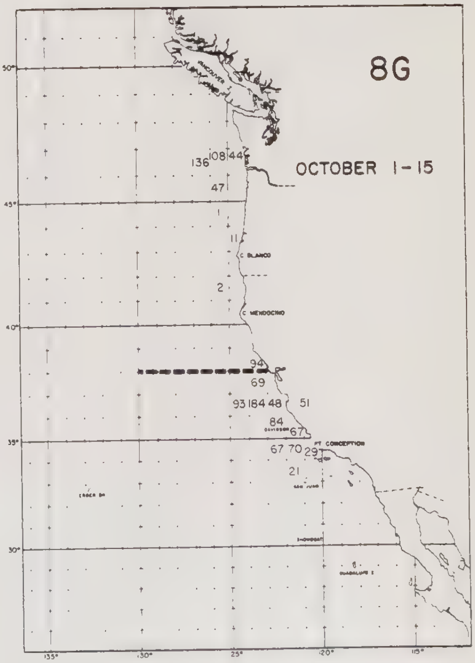

8B
JULY 16-31
VANCOUVER ISLAND
101
326
153 139 62
272 196 162
179 280 183 84
243 279 273
100
C. BLANCO
296
7
C. MENDOCINO
DAVIDSON
PT CONCEPTION
SAN JUAN
3 .6 15
34 60
SHOWBOAT
GUADALUPE I.
ERBEN BK.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


8C
AUGUST 1-15
VANCOUVER ISLAND
87
213 225 185 35
322 224 141 105
174 230 50 202
6 207 162 100 160
177 162 117 10
147 167 246 55 135
C. BLANCO
126 27 126
53
C. MENDOCINO
321
82
227
DAVIDSON
237
PT CONCEPTION
2
SAN JUAN
25 .7
28 2
SHOWBOAT
GUADALUPE I.
ERBEN BK.
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


8D
AUGUST 16-31
VANCOUVER
C BLANCO
MENDOCINO
PT CONCEPTION
SAN JUAN
CORTES BK
GUADALUPE I
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


8E
SEPTEMBER 1-15
VANCOUVER
C BLANCO
MENDOCINO
PT CONCEPTION
SAN JUAN
CORTES BK
GUADALUPE I
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


8F
SEPTEMBER 16-30
VANCOUVER
C BLANCO
MENDOCINO
PT CONCEPTION
SAN JUAN
CORTES BK
GUADALUPE I
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


8G
OCTOBER 1-15
VANCOUVER
C BLANCO
C MENDOCINO
PT CONCEPTION
SAN JUAN
CORTES BK
GUADALUPE I
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

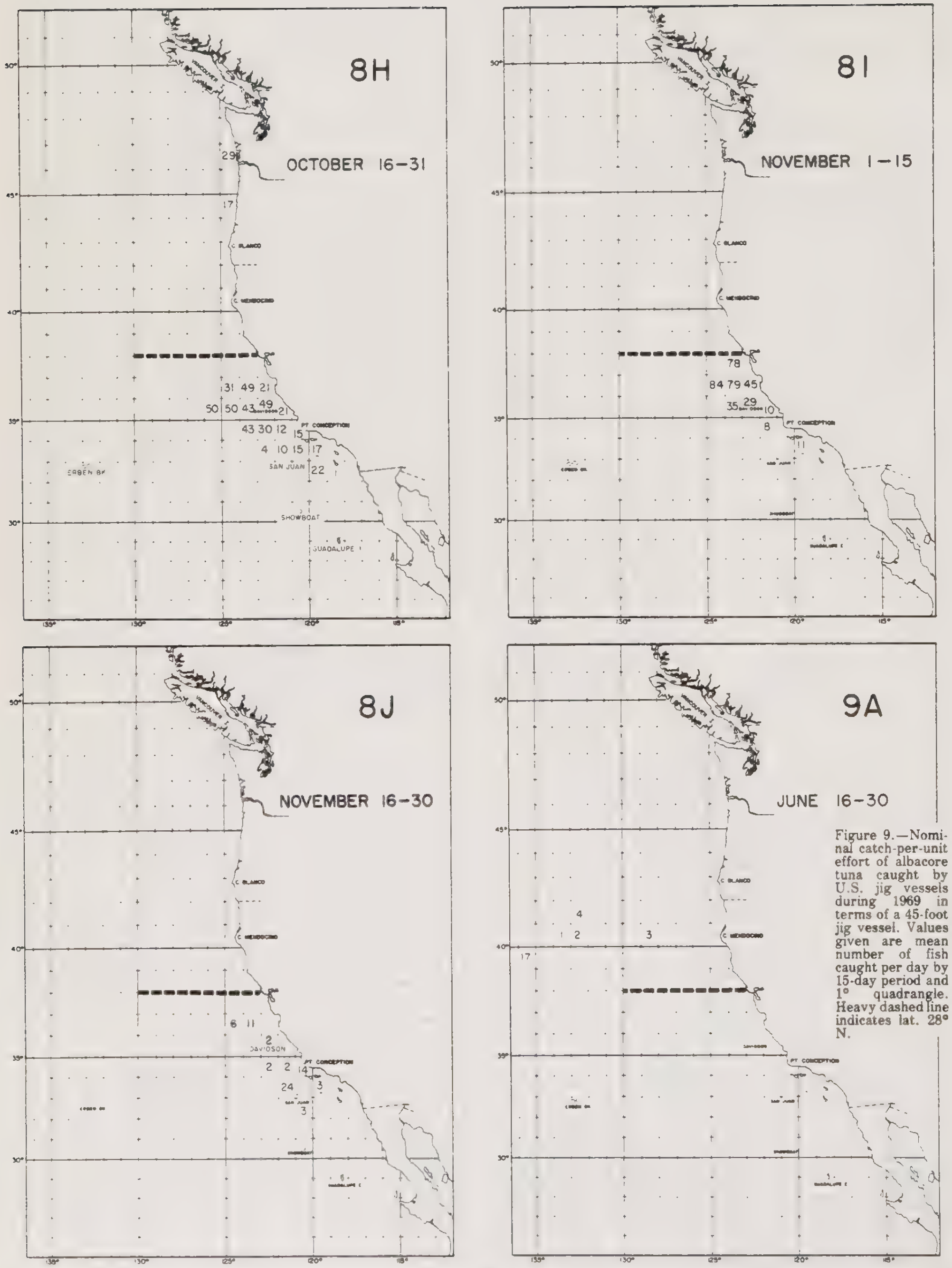
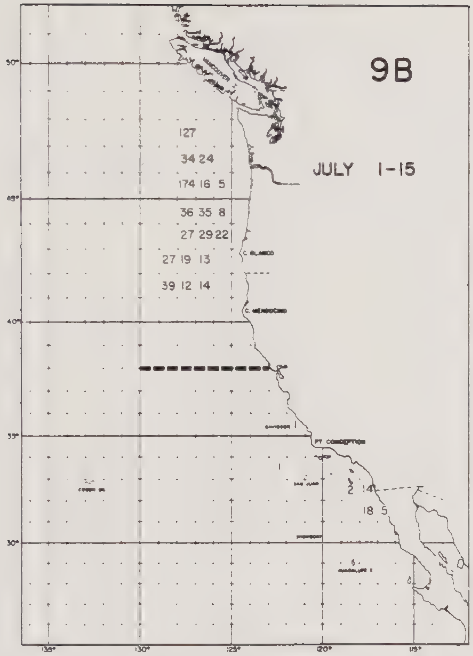
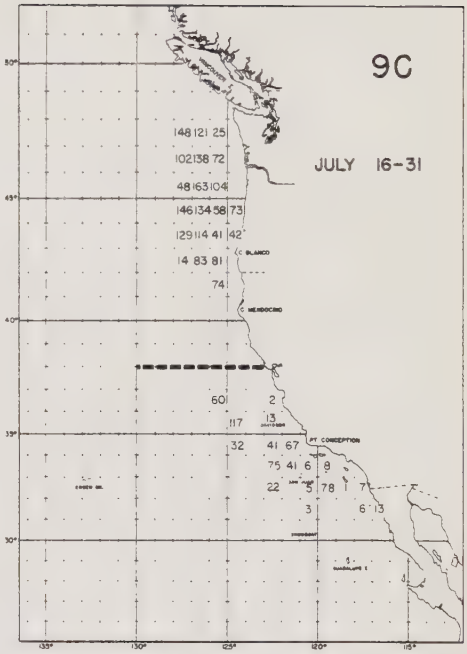
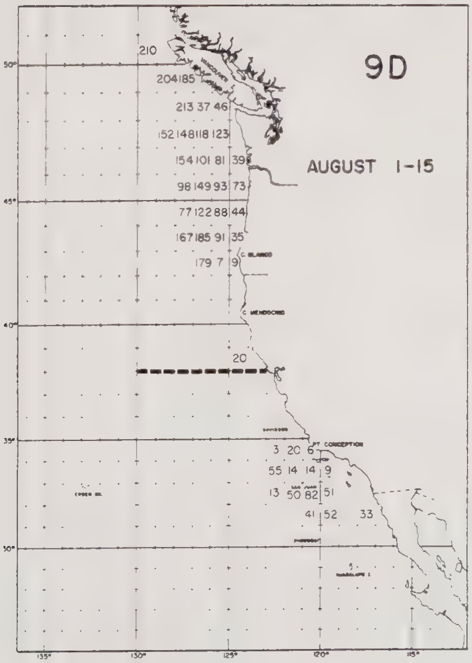
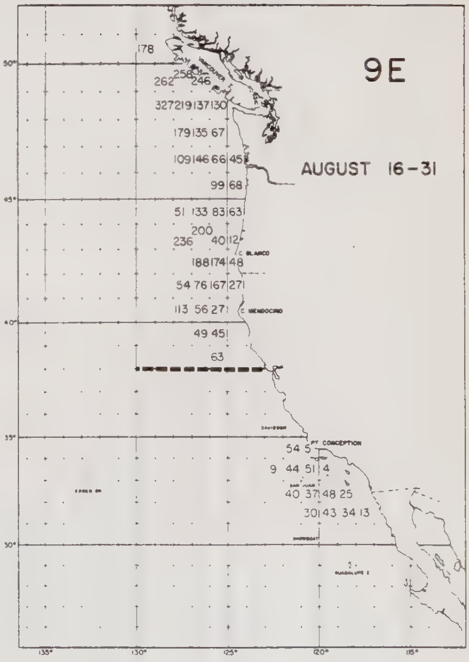

8H
OCTOBER 16–31
29
17
C. BLANCO
C. MENDOCINO
31 49 21
50 50 43 49 21
43 30 12
15
PT CONCEPTION
4 10 15 17
SAN JUAN
22
ERBEN BK
SHOWBOAT
GUADALUPE I
8I
NOVEMBER 1–15
78
84 79 45
35 29 10
8
11
8J
NOVEMBER 16–30
6 11
2
DAVIDSON
2 2 14
3
24
3
9A
JUNE 16–30
4
1 2
3
17
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°

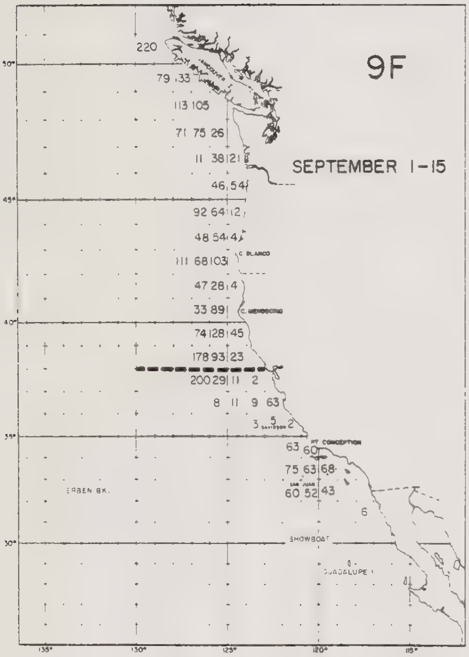
Figure 9.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1969 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 28° N.


9B
JULY 1-15
127
34 24
174 16 5
36 35 8
27 29 22
27 19 13
39 12 14
1
1
2 14
18 5
C. BLANCO
C. MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


9C
JULY 16-31
148 121 25
102 138 72
48 163 104
146 134 58 73
129 114 41 42
14 83 81
74
60
2
117
13
32
41 67
75 41 6 8
22
5 78 1 7
3
6 13
C. BLANCO
C. MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


9D
AUGUST 1-15
210
204 185
213 37 46
152 148 118 123
154 101 81 39
98 149 93 73
77 122 88 44
167 185 91 35
179 7 9
20
3 20 6
55 14 14 9
13 50 82 51
41 52 33
C. BLANCO
C. MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


9E
AUGUST 16-31
178
262 258 246
327 219 137 130
179 135 67
109 146 66 45
99 68
51 133 83 63
200
236 40 12
188 174 48
54 76 167 271
113 56 271
49 45
63
54 5
9 44 51 4
40 37 48 25
30 43 34 13
C. BLANCO
C. MENDOCINO
PT CONCEPTION
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°


9F
SEPTEMBER 1-15
VANCOUVER I.
C. BLANCO
C. MENDOCINO
DAVIDSON
PT CONCEPTION
SAN JUAN
ERBEN BK.
SHOWBOAT
GUADALUPE I
220
79 33
113 105
71 75 26
11 38 121
46 54
92 64 12
48 54 4
111 68 103
47 28 4
33 89
74 128 45
178 93 23
200 29 11 2
8 11 9 63
3 5 2
63 60
75 63 68
60 52 43
6
50°
45°
40°
35°
30°
135°
130°
125°
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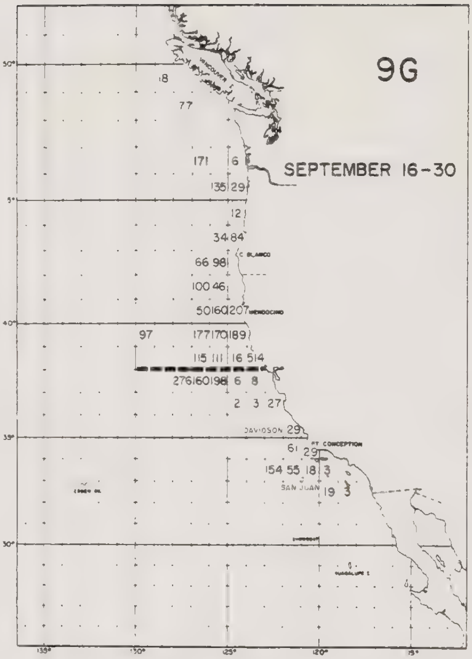
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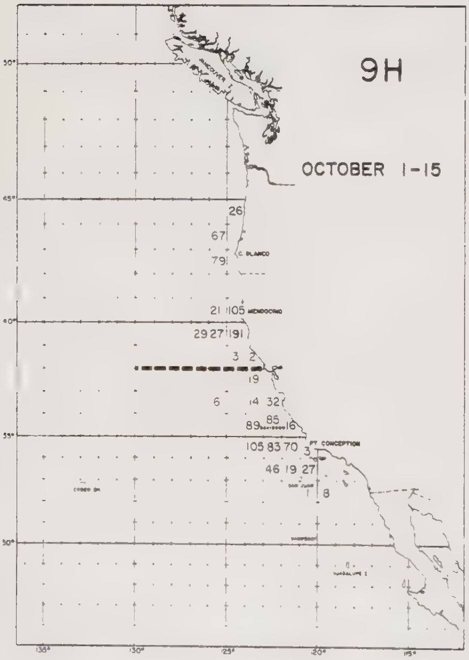
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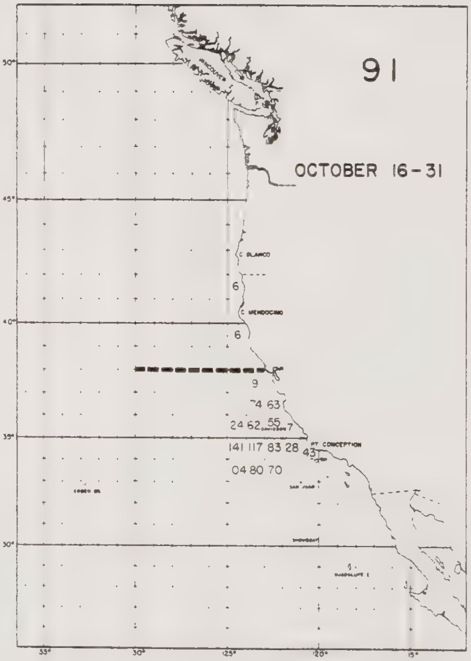
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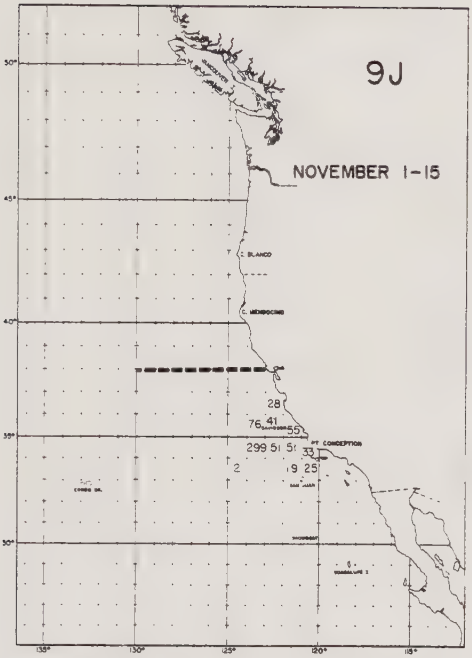
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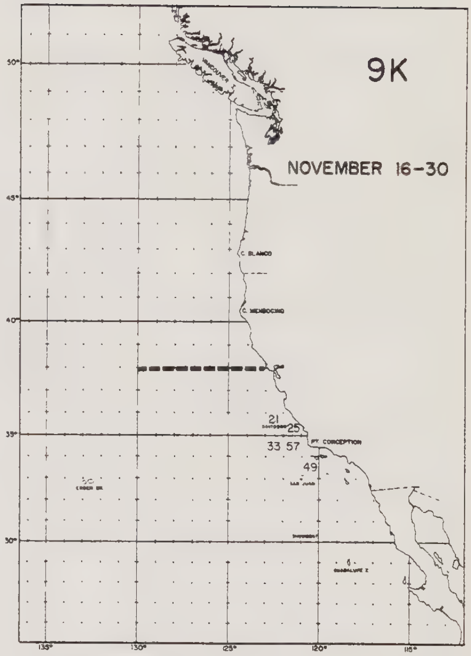
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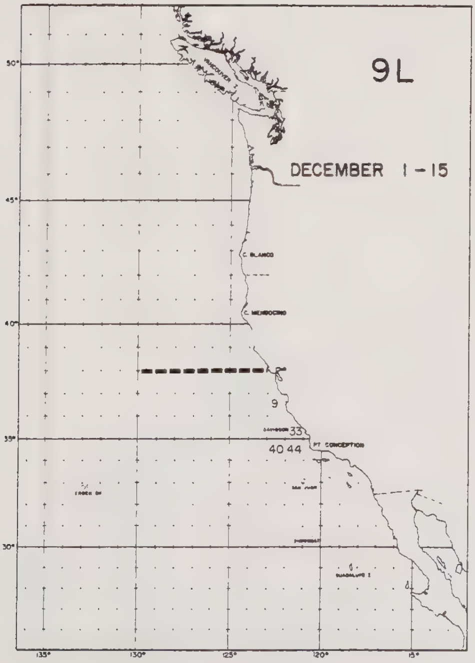
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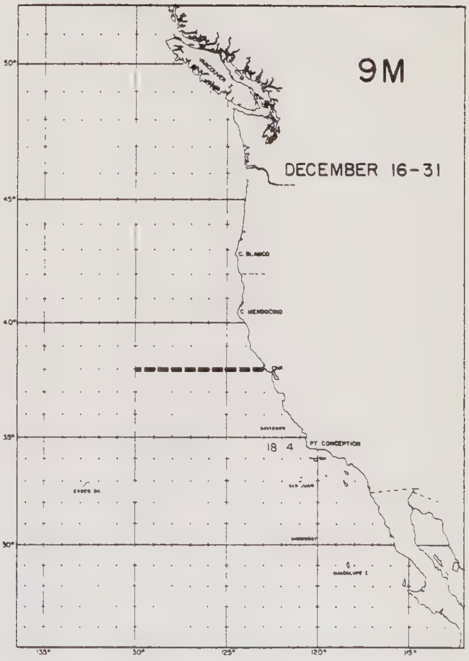
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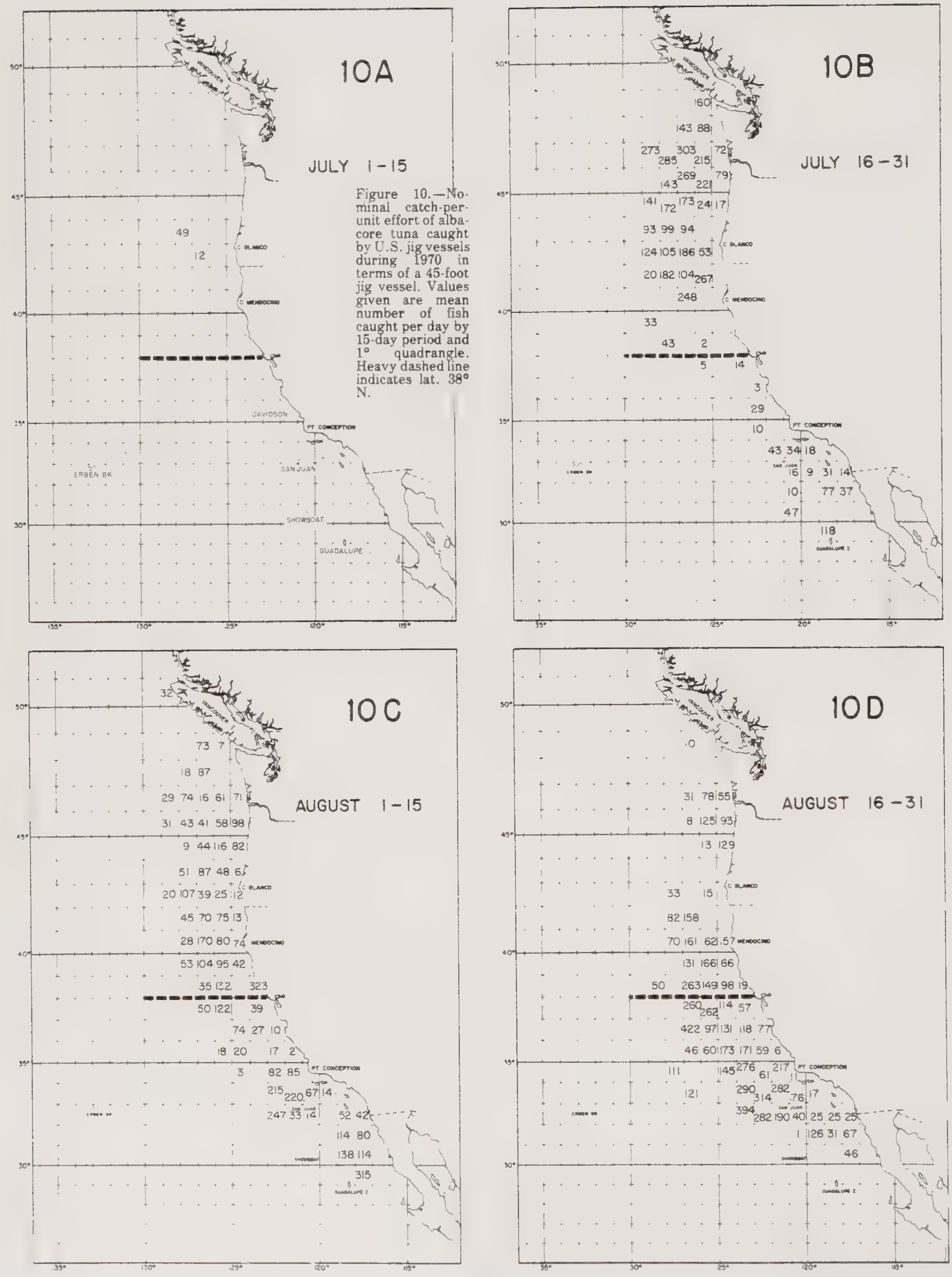
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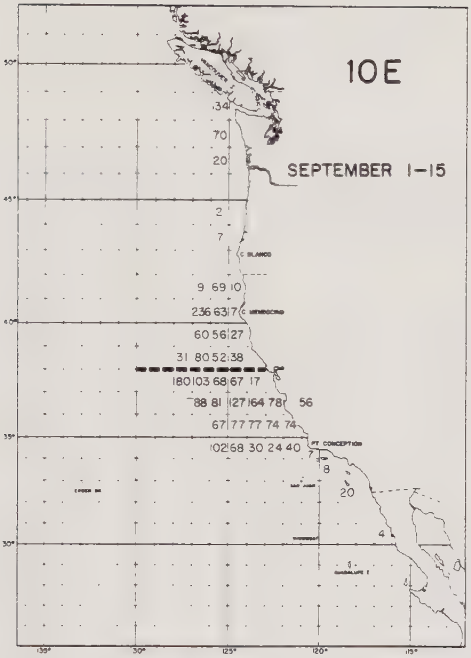
Figure 10.—Nominal catch-per-unit effort of albacore tuna caught by U.S. jig vessels during 1970 in terms of a 45-foot jig vessel. Values given are mean number of fish caught per day by 15-day period and 1° quadrangle. Heavy dashed line indicates lat. 38° N.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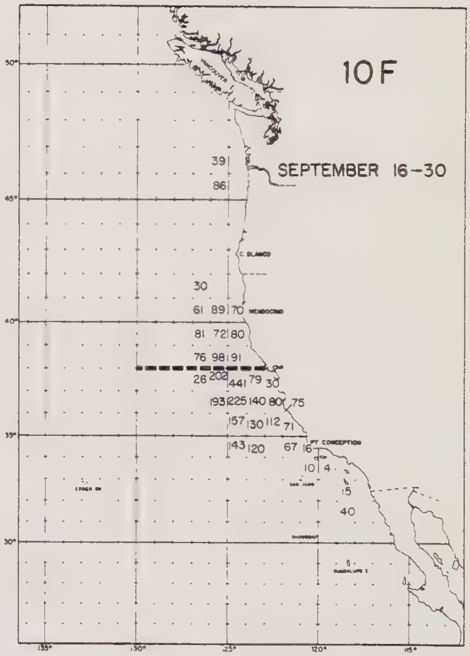
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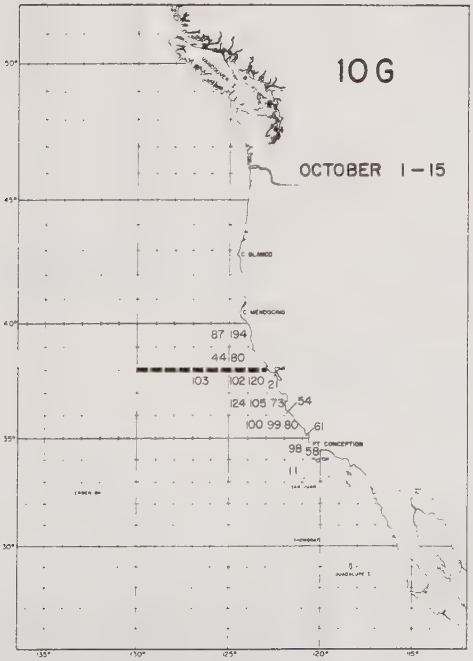
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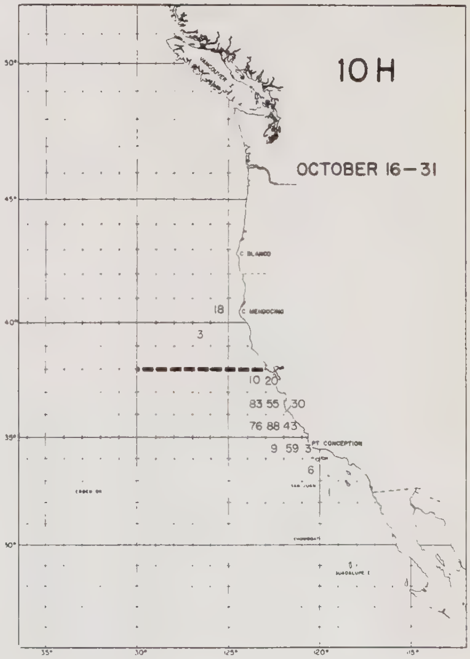
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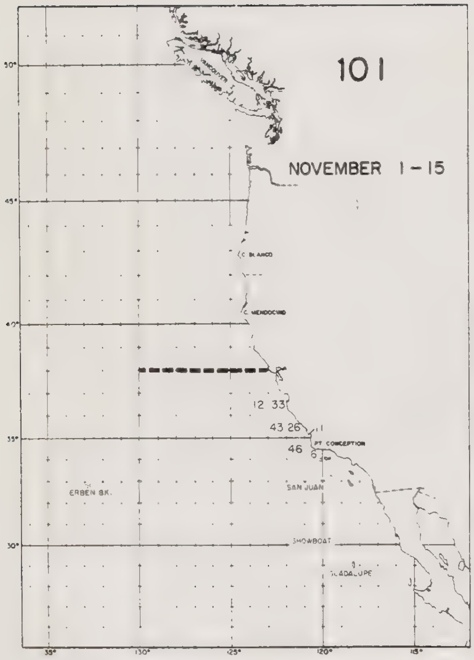
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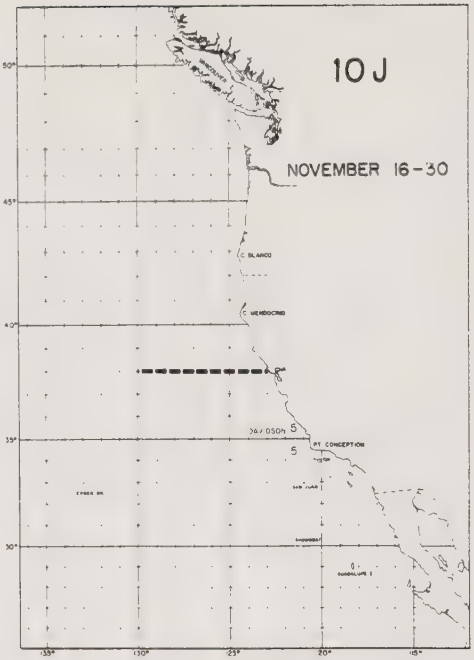
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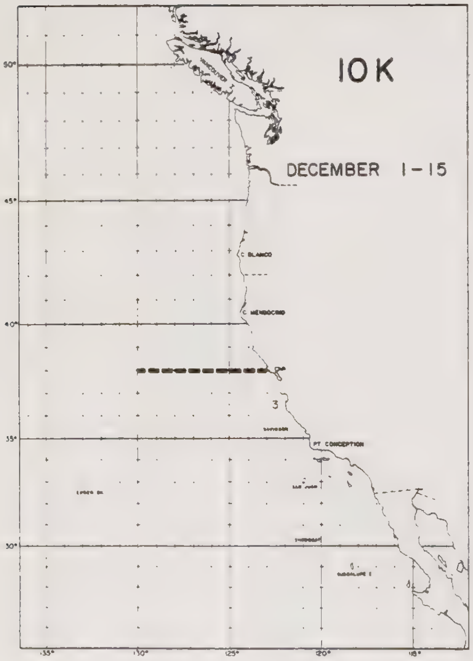
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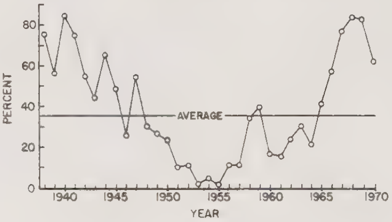
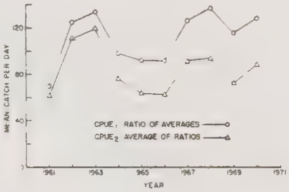


Figure 11.—Percentage of the west coast albacore tuna catch taken north of San Francisco (lat. 38°N) for years 1938-1970.

Figure 12.—Nominal catch-per-unit effort for albacore tuna caught by U.S. jigboats.



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ESTIMATES OF RATES OF TAG SHEDDING BY NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*

R. MICHAEL LAURS, WILLIAM H. LENARZ, AND ROBERT N. NISHIMOTO[1]

ABSTRACT

Type-I (immediate) and Type-II (instantaneous) rates of tag shedding by North Pacific albacore, *Thunnus alalunga*, are estimated using data from a double-tagging experiment. Type-I shedding is estimated to be about 0.12 and Type-II to be between 0.086 and 0.098 on an annual basis. The paper also contains a discussion on the accuracy of the estimates, and a method is developed to estimate possible bias due to fishermen reporting double tag recoveries as single tag recoveries. The possible bias is estimated to be low.

A tagging program was initiated in 1971, and is continuing, on North Pacific albacore, *Thunnus alalunga* (Bonnaterre), to examine their migration patterns, to obtain information for use in population studies, and to estimate rates of mortality. Because loss of tags through shedding can cause estimates of mortality to be biased upwards unless corrected for, part of the tagging program in 1972 consisted of an experiment in which 788 albacore were double-tagged to evaluate tag shedding by this species.

Chapman et al. (1965) developed a formulation of the return of single- and double-tagged fish which includes instantaneous loss rates due to fishing mortality, other mortality, and tag shedding. They then solved for the instantaneous rate of tag shedding given data from double-tagging experiments. Bayliff and Mobrand (1972) extended the work of Chapman et al. to provide estimates of the portion of tags which are retained after immediate shedding occurs. Results of the use of the Bayliff and Mobrand procedure to estimate rates of tag shedding from the double-tagging experiment on North Pacific albacore are presented in this paper.

METHODS

The tagging program is being conducted jointly by the National Marine Fisheries Service[2] (NMFS), NOAA, and the albacore fishing industry through the American Fishermen's Research Foundation[3] (AFRF).

Albacore were caught by commercial jig boats and a bait boat on charter to the AFRF. Fishing operations on jig boats were conducted with standard commercial albacore feathered jig-fishing equipment and commercial trolling methods. Most of the fish that were tagged and released from the bait boat were caught by the "winging" method of live-bait, pole-and-line fishing, whereby a fish is caught on an anchovy-baited barbless hook on the end of a short line attached to a stout pole. Immediately after hooking, the fish is lifted out of the water, swung toward the fisher, and caught under the arm of the fisher, who then removes the hook. A small number of the fish tagged from the bait boat were taken by trolling feathered jigs and on rod-and-reel using live anchovy as bait.

Special care was exercised to tag and release only fish judged to be in very good condition. Fish which showed signs of severe bleeding, which were hooked through the roof of the mouth or which showed signs of extreme exhaustion, were not tagged. For each tagged and released fish records were kept of the number of the tag, the date and time of tagging, the length of fish to the nearest lower centimeter, condition of fish, and sea surface temperature. A fish caught by pole and line was measured with a large caliper and tagged with two tags inserted almost simultaneously by a technician while the fisher held the fish under his arm. A fish caught on trolling gear and rod-and-reel was

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038. Authorship is alphabetical. Laurs was the investigation leader and responsible for the overall tagging program and was aided by Nishimoto. Lenarz was responsible for the analytical aspects of the study.

[2] Southwest Fisheries Center, La Jolla, CA 92038.

[3] AFRF administers revenues derived from an assessment paid on U.S. - landed albacore.

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measured on a Naugahyde-covered foam measuring pad and tagged by a technician while it was on the pad. In order to tag an albacore on each side, using this method, the fish had to be turned from side-to-side.

Spaghetti-dart type Floy[4] tags are being used in the tagging program. The tags are made of yellow Resinite tubing, 12 to 13 cm long and similar in structure to those described by Yamashita and Waldron (1958) and identical to those used by Fink (1965). The tags were inserted on both sides of the fish below the second dorsal fin with the aid of a beveled stainless steel piece of tubing, 14 to 16 cm long and 0.135- or 0.156-inch inside diameter. The tags were inserted so that the barb of the tag was lodged around the pterygiophores of the second dorsal fin.

We estimated rates of tag shedding using the notation and methodology of Bayliff and Mobrand (1972) for yellowfin tuna as did Lenarz et al. (1973) in a similar study on bluefin tuna. Bayliff and Mobrand's equations for returns of tags are:

$$n_{ddk} = F\tau N_D \pi \rho^2 e^{-(F + X + 2L)t_k} \tag{1}$$

and

$$n_{dsk} = 2F\tau N_D \pi\rho \, (1 - \rho e^{-Lt}k) e^{-(F + X + L)t_k} \tag{2}$$

where

t_k = time at the middle of the kth recovery period of length τ days ($k = 1, 2$);

n_{ddk} = number of returns of double-tagged fish retaining both tags during the period centered at t_k;

n_{dsk} = number of returns of double-tagged fish retaining only one tag during the period centered at t_k;

N_D = number fish released with double tags;

π = portion of tagged fish which remain alive after the immediate mortality, including Type I tagging mortality, has taken place;

ρ = portion of the tags which are retained after Type-I (immediate) shedding has taken place;

F = instantaneous rate of fishing mortality;

X = instantaneous rate of other mortality (other included natural mortality, Type-II (long-term) tagging mortality, and apparent mortality due to migrations from the fishery); and

L = instantaneous rate of tag shedding (Type-II shedding).

Bayliff and Mobrand (1972), using Equations (1) and (2), showed that

$$\ln \frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = -Lt_k + \ln \rho = y_k \tag{3}$$

where y_k is an estimate of the natural logarithm of the proportion of tags retained up to time t_k. Note that the first factor of the right-hand side of Equation (2) is the integer 2. Both Bayliff and Mobrand (1972) and Lenarz et al. (1973) mistakenly left this multiplier out of the equation in their papers. However, the error was typographical and did not affect their derivations or results. Given n_{ddk}, n_{dsk}, and t_k, L and ρ are estimated using simple linear regression; or as in the case of this study when only two recovery periods are used, the solution of two simultaneous equations. Equations (1) and (2) assume that L and the total of F and X are constant over t_k. Since the albacore fishery is seasonal, the assumption is likely to be violated. The effect of the violation has not been examined.

RESULTS

Release and return data through 1973 are shown in Table 1. The number of returns in 1974 was insufficient for analysis. A chi-square test indicated that gear type did not have a significant effect on the proportions of single- and double-tag returns in 1972 ($\chi^2 = 1.117$, df $= 1$). Data from both gears were combined for the remainder of the analysis.

Estimates of ρ and L are shown in Table 2. Only returns that could be specified to the nearest week are included in Table 1. Precise dates of recovery

TABLE 1.–Tag releases and returns with information on date of recovery for North Pacific albacore and double-tag study.

Gear type	1972 double-tag releases	1972 returns			1973 returns		
		Double (n_{dd1})	Single (n_{ds1})	Average days out (t_2)	Double (n_{dd2})	Single (n_{ds2})	Average days out (t_2)
Jig	330	10	5	—	12	5	—
Bait	448	22	5	—	2	3	—
Total	778	32	10	54.71	14	8	451.55

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[4] Floy Manufacturing Company, Seattle, Wash. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.–Estimates of rates of tag shedding, $\hat{L}$ (on an annual basis), retention, $\hat{\rho}$, from 1972 North Pacific albacore double-tag study.

Item	$\hat{L}$	$\hat{\rho}$
Undated returns excluded	0.098	0.88
Undated returns included	0.086	0.88

TABLE 3.–Tag releases and returns from North Pacific albacore single-tag studies.

Year of release	Number released	Number returned 1971	1972	1973	1974
1971	887	0	16	11	6
1972	1,304		27	47	14
1973	1,806			13	59
1974	2,490				35

could not be assigned to seven double-tag and two single-tag returns in 1972 and one double-tag return in 1973. We assumed that t_k was the same for the returns shown in Table 1 and the returns with unspecified recovery dates and included the 10 additional returns in a recalculation of $\hat{\rho}$ and $\hat{L}$ The results of the recalculations are similar to the original (Table 2). We estimated ρ to be about 0.88 and L on an annual basis to be between 0.086 and 0.098. This means that if no mortality occurs, 8.2 to 9.3% of all unrecovered tags are expected to be lost through shedding annually.

Our estimate of ρ is similar to the results obtained for yellowfin tuna ($\hat{\rho}$ = 0.913) by Bayliff and Mobrand (1972) and bluefin tuna ($\hat{\rho}$ = 0.973) by Lenarz et al. (1973). However, our estimate of L is considerably lower than that obtained for yellowfin tuna ($\hat{L}$ = 0.278) and bluefin tuna (L = 0.310).

Methodology for estimation of the variance of L and ρ when only two periods of recovery are available has not been published. However, we believe that the number of tag returns available for this study is too low for accurate estimates of ρ and L. We made the following calculations to illustrate the relative level of accuracy. If we arbitrarily assume that the returns of double- and single-tagged fish in 1973 were from a binomial distribution with the probability of a returned fish having only one tag being 0.5, the probability of having 8 or fewer fish returned with only one tag out of a sample of 22 fish from such a population is about 0.14. If 11 fish were returned with single tags (the expected value from the assumed distribution) instead of the 8 observed, our estimates of ρ would be 0.895 and our estimate of L would be 0.172. Thus it appears that there is a reasonable chance that our estimate of L (about 0.09) could be considerably lower than the true value.

We are not aware of any other data available from double-tag studies on albacore. However, there is a considerable amount of data available from single-tag studies conducted in recent years on albacore in the eastern North Pacific (Table 3). Return rates in the year after release were 0.018 for the 1971 releases, 0.036 for the 1972 releases, and 0.033 for the 1973 releases of single-tagged fish, for an average of 0.029. If the return rates are divided by 0.88 to account for Type-I tag shedding, the average becomes 0.033. The return rate in the year after release for the double-tag study was 0.027. If the rate is divided by 0.99 $(1 - (1 - \hat{\rho})^2)$ to account for Type-I shedding of both tags, the return rate is 0.027. Thus the return rates from the single-tag studies give further evidence that Type-II shedding is insignificant, because if it were not, return rates adjusted for Type-I shedding from the single-tag releases should be lower than return rates from the double-tag releases, provided mortality rates were similar for these years.

The above estimates are based on the assumption that all double-tag recoveries are reported as double-tag recoveries. A possible source of error is that some fishers may return only one tag from a double-tag recovery. These fishers might return only one tag because of their interest in albacore migrations, but retain the second tag as a souvenir. This would result in our underestimating the value of ρ. To illustrate the extreme case assume that ρ is actually 1.0, but we estimate it to be 0.88 because of incomplete reporting. Then assuming ρ = 1, Equations (1) and (2) become

$$n_{ddk} = F \tau N_D \pi Be^{-(F + X + 2L)t_k} \tag{4}$$

and

$$n_{dsk} = 2F \tau N_D \pi (1 - e^{-Lt}k)e^{-(F + X + L)t_k} + (1 - B) F \tau N_D \pi e^{-(F + X + 2L)t_k} \tag{5}$$

where B = minimum proportion of double-tag recoveries that are reported as double-tag recoveries.

Manipulation of Equations (4) and (5) results in

$$\frac{(n_{dd2} + n_{ds2})(n_{dd1})}{(n_{dd1} + n_{ds1})(n_{dd2})} = \frac{2e^{Lt_2} - 1}{2e^{Lt_1} - 1} \tag{6}$$

and

$$B = \frac{(2e^{Lt_k} - 1)(n_{ddk})}{n_{ddk} + n_{dsk}}. \qquad (7)$$

An estimate of L is obtained from an iterative solution of Equation (6). An estimate of the minimum value of B is obtained from substitution of the estimate of L into Equation (7). Our estimate of L and the minimum value of B, where only returns with specified dates are included in the calculations, are 0.087 and 0.78, respectively. When all of the return dates are included we estimate L to be 0.077 and B to be 0.78. Thus, it appears that the rate of reporting double-tag recoveries as single-tag recoveries is less than 0.22 $(1 - B)$.

However, we have no evidence to indicate that fishers have returned only one tag from fish recovered with two tags. We believe that fishers have turned in both tags of fish recovered with two tags based on interviews with those who have recovered tagged fish, the very good cooperation that we have received from them during the tagging program, and the fact that tags from recovered fish may be returned to the fisher if he wishes to have them.

ACKNOWLEDGMENTS

We thank the skippers, crewmen, and NMFS technicians who participated in the albacore tagging and release program; members of AFRF for supporting the tagging charters; albacore fishers and fish processors for their excellent cooperation in reporting tag recoveries. We also thank R. Francis of the Inter-American Tropical Tuna Commission, J. Wetherall of the Southwest Fisheries Center Honolulu Laboratory, and J. Zweifel of the Southwest Fisheries Center La Jolla Laboratory, for critically reviewing the paper. J. Wetherall and M. Yong have developed maximum likelihood estimators of the variance of $\hat{\rho}$, $\hat{L}$, and $\hat{B}$ and intend to publish their work.

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Three Computer Simulation Games for the Instruction of Population Dynamics

Hiram W. Li and Peter B. Adams

Computer simulated gaming has been suggested by several scientists as a training device for students of resource management (Paulik 1969; Schreck and Everhart 1973; Titlow and Lackey 1974). Through this type of interaction, students begin to appreciate concepts upon which management strategies are based. We have developed three games—TUNA, SALMON, and PLAICE—that simulate the dynamics of Eastern Pacific tropical tuna, Skeena River sockeye salmon, and North Sea plaice. The games are based upon Schaefer's (1954) surplus yield model, Ricker's (1958) spawner-recruit model, and Beverton and Holt's (1957) dynamic pool model, respectively. Economic data for the models were taken from the National Marine Fisheries Service's Statistical Digest series. The primary objective of the games is to place the student in a situation where decisions governing the exploitation of a fishery are made in a realistic setting. Cultural factors influencing management decisions have been incorporated into the games in order to expose the student to the multiplicity of interactions that influence fisheries policy. However, we consciously decided to give only a flavor of the real world so that the students would base most of their decisions upon biological factors. Students are encouraged to test the sensitivity of the population's dynamics to different factors in the game by varying one component while holding others constant. By doing so, the students learn more about the assumptions upon which the models are based.

Students enter into the game in a realistically blind situation; that is, the student has to decide upon a management strategy. Students can learn how to optimize exploitation empirically, but soon realize that understanding the theoretical model increases their efficiency. Each game iterates a given number of times the length of the resource manager's contract. At the end of the game, data are also presented in graphical form. The student receives additional feedback in forms of "memos" and "directives" from "superiors." We have found that time-share games eliminate or reduce the frustrations of the punch card or batch approach. Extensive background in computers or computer languages is unnecessary to play these games.

The games are written in BASIC and FORTRAN IV. Complete listings, documentation, and additional information are available from the authors.

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FISHERIES RESOURCES AND STUDIES

(*Condensed from* TVA '75 Annual Report, Vol. I-TEXT.)

Although nearly 17 million one-day fishing trips are taken on TVA lakes each year, the region's fishing resources are still underutilized. TVA fish biologists estimate that the lake system could yield double the current harvest, or 30 million pounds.

TVA periodically conducts inventories of fish populations, water quality, invertebrates, and plant life in lakes and streams. The Norris Study, a fish-sampling inventory on the Norris Reservoir, is recording fish distribution at various depths throughout the year.

The Biothermal Laboratory at Browns Ferry Nuclear Plant in northern Alabama—a joint ten-year project of TVA and EPA—has begun studying the effects of heated water on fish and other organisms in the Wheeler Reservoir. Shallow reservoir habitat, including rock-bottom rubble and shoals, is simulated in twelve raceways filled with Wheeler Reservoir water continuously pumped, and warmed by the discharge from the Browns Ferry Plant. In addition to the natural colonization of micro-organisms, invertebrates, and algae, selected fish species common to the southeastern United States are stocked in the raceways.

Scientists will study survival, growth, and reproduction under various water temperatures and make their findings available to other agencies and organizations.

Deep-Sea Research, 1976, Vol. 23, pp. 729 to 754. Pergamon Press. Printed in Great Britain.

Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean

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Abstract—Data from 86 detailed zooplankton profiles taken during the EASTROPAC cruises of 1967 to 1968 have enabled a first-order description to be made of zooplankton distribution in the upper 1000 m of the water column in relation to density, light, oxygen, and phytoplankton. A layer of abundant epiplankton contains a subsurface maximum that tends to coincide with the bottom of the mixed layer and with the depth of maximum carbon fixation, but lies above the chlorophyll-*a* maximum. Zooplankton abundance declines sharply downwards across the pycnocline, forming a discontinuity between the epiplankton and the low-biomass plankton below. Coincident with the deep sonic scattering layers are diurnal layers of migrant interzonal species which rise at night into the epiplankton. Major regional differences are caused by the shoaling of the pycnocline at the equatorial divergence, and the very deep pycnocline of the southern gyral region. An hypothesis, based upon the EASTROPAC data, is stated: that the form of phytoplankton profiles, in periods or regions of stable production, may be primarily determined by a depth-differential in herbivore grazing pressure, rather than by differential cell-sinking rates as is suggested in classical production models.

INTRODUCTION

ZOOPLANKTON abundance in low latitudes appears to be greatest in a relatively shallow layer which is separated from water containing much less zooplankton at some depth between 100 and 300 m. VINOGRADOV (1968) reports many zooplankton profiles for low Pacific latitudes in which plankton abundance decreases by about an order of magnitude between the surface and 1000 m to a very low biomass, which is itself reduced by another order of magnitude only between 3000 and 5000 m. It is also evident from these profiles that biomass in the upper kilometre of the water column contains a discontinuity at some depth above 500 m, at which most of the decrease occurs. Such a discontinuity may occur elsewhere in the oceans, though its depth varies considerably (e.g. FOXTON, 1956; GRICE and HULSEMANN, 1965).

It is predictable that zooplankton profiles should contain a degree of complexity to match what is well known to occur in pumped phytoplankton profiles; however, because of the restrictions imposed by opening–closing nets for zooplankton collection, only very rarely have zooplankton profiles been obtained of comparable resolution to profiles of phytoplankton and its related variables, which can be obtained by pumps with much less expenditure of ship-time; commonly, only about five levels are sampled down to about 500 m with opening–closing nets (e.g. VINOGRADOV, 1968). When higher resolution has been obtained, as with the new series of RMT1 and RMT8 nets (BAKER, CLARKE and HARRIS, 1973), several hours are required to obtain a single profile, during which period vertical migration may to some extent occur even if twilight is avoided, and it is usually impossible to work many such stations during one cruise or survey.

For these reasons, the number of stations for which we have zooplankton profiles of high resolution is relatively small, and although the details of plant and animal profiles must, in fact, be causally matched by the processes of grazing and regeneration of nutrient salts, we have not advanced much farther in our interpretation of these relations than the models of RILEY, STOMMEL and BUMPUS (1949) and of STEELE and YENTSCH

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(1960) in which grazing was considered to be a uniform factor throughout the euphotic zone—which it clearly is not.

The EASTROPAC expeditions in 1967 to 1968 were designed to monitor seasonal change in a large part of the eastern tropical Pacific Ocean, between about 20°N and 20°S; cruise and station numbers used in the present paper are the same as presented in the EASTROPAC Atlases (LOVE, 1971). Zooplankton hauls with multiple serial plankton samples (LONGHURST, REITH, SEIBERT and BOWER, 1966), or Longhurst–Hardy Plankton Recorders (LHPR's), as they have come to be called, were included in standard EASTROPAC station procedures together with profiles of plant pigments, carbon fixation, inorganic nutrients, oxygen, transparency and physical variables; all station and data processing procedures are described by LOVE (1971). These data enable us to examine, over a very large area of the ocean and over all seasons, the relationships between profiles of zooplankton and other variables in the upper kilometre of the water column.

For the purposes of this investigation it was assumed that net-caught zooplankton were predominantly herbivores (p. 749); it was further assumed, except in some special cases discussed separately, that carnivores would aggregate, in general, at similar depths to their herbivore prey.

DATA ACQUISITION

The zooplankton profiles were taken with 0.5 m^2 LHPR equipment, fitted with 0.3 mm nylon filtering gauze. Successful profiles were obtained at 86 stations (Fig. 1) during four cruises of the *David Starr Jordan*, as follows:

EASTROPAC cruise
12—February–March 1967—32 stations
30—June–July 1967—20 stations
60—December–January 1967-68—21 stations
76—March 1968—13 stations.

All stations were worked within about one hour of midday and midnight in order to sample only when diel migrants were at their most stable in respect of depth levels, and to avoid the dusk and dawn periods of relatively very rapid vertical movement. Even though, as ROE (1974) has recently confirmed, some vertical shifts occur during the periods of full daylight and darkness, midday and midnight levels effectively represent the depth at which diel migrants spend most of their time.

The standard LHPR haul comprised a single oblique profile to the surface; the gear was sunk as rapidly as possible, usually in little more than 5 min, until it was judged that it had reached 500 m, at which depth it was held for 2 min to stabilize itself. It was then hauled slowly and obliquely to the surface with about 50 sampling periods, each of 30-s duration, giving an average sampling depth interval of 9.3 m and a total hauling time of about 30 min. There were 73 such standard stations on cruises 12, 30 and 60, which were found subsequently to have varied from 200 to 700 m in sampling depth, though half fell within the range 450 to 500 m. In addition, on cruise 76 there were 10 special shallow hauls designed to give greater resolution within the mixed layer; these had an average sampling depth interval of only 2.5 m between the surface and depths of 150 to 300 m. Finally, on the same cruise three special deep hauls from 1000 m were worked successfully.

The total number of individual plankton samples from these 86 stations was 3886, each representing about 10 m^3 filtered; the actual amount filtered and the sampling depth intervals were recorded for each sample by the instrument, and used to normalize the data. The LHPR equipment had no bridles in front of the net aperture and was coloured black: these measures appear to have so reduced net-avoidance by zooplankters that no consistent day/night ratio could be detected in numbers of organisms per cubic metre, and the problems discussed by BRINTON (1967) were apparently not important.

The plankton nets and recorder were carefully examined on recovery; whenever serious hang-up of organisms on the nets was found to have occurred, the haul was rejected, as were hauls in which subsequent sample editing showed that entrainment of specimens in the recorder had occurred. Rejected hauls were about 10% of all hauls taken, and are not listed here.

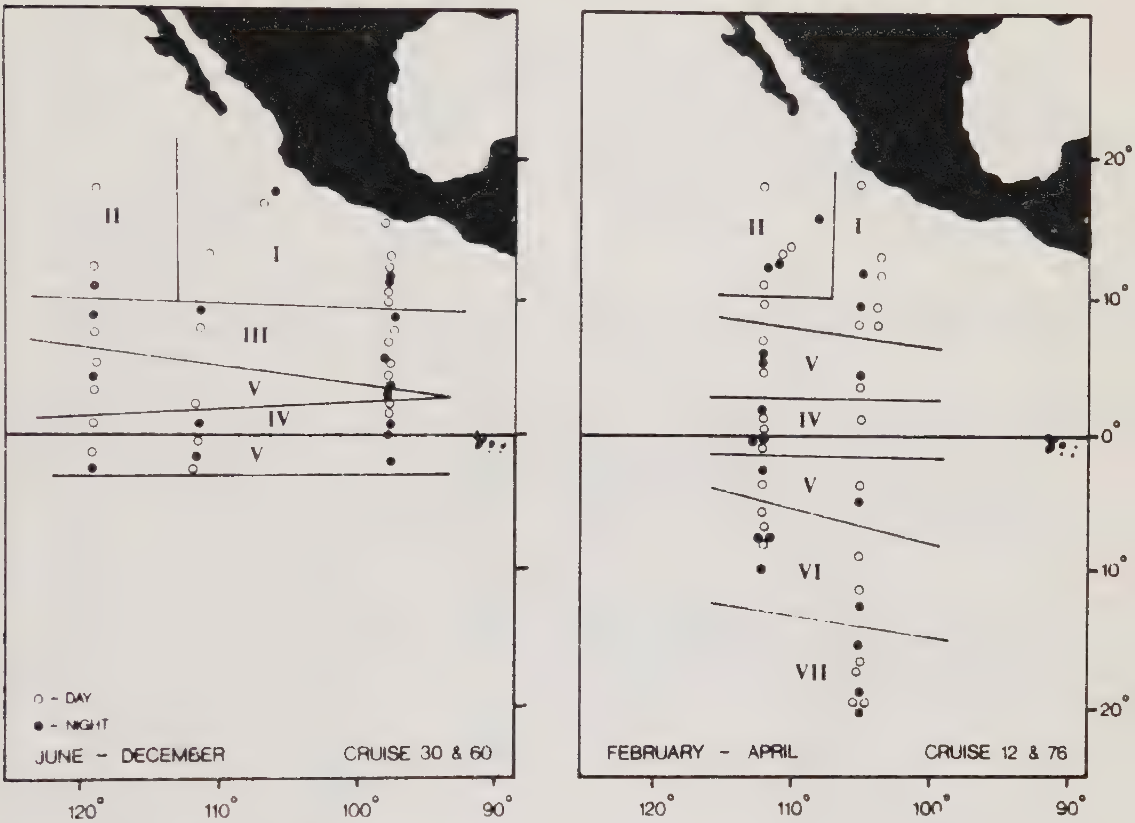

Fig. 1. Location of LHPR profiles and allocation of stations to oceanographic regions I to VII; open circles— midday stations, closed circles—midnight stations.

The samples were subsequently sorted into 18 major categories (all coelenterates, all copepods, chaetognaths, molluscs, cladocera, etc.) and 18 minor categories including some genera (e.g. *Euchaeta*, *Eucalanus*, *Candacia*), some artificial groups (e.g. large and small species of *Pleuromamma*) and some single species (e.g. *Rhincalanus nasutus*, *R. cornutus*, *Euphausia diomediae*, *E. gibboides*). Twenty-one profiles from cruise 12 were sorted for six species of *Clausocalanus* as part of a different investigation: these data are included in those considered here. Biomass, expressed as dry weight in mg m^{-3}, was computed from volumetric measurements made on each sub-sample using factors experimentally derived for 10 categories of zooplankton composition as sampled by the auxiliary net fitted to the LHPR (Longhurst, Reith, Seibert and Bower, 1966); each sub-sample was allocated to the zooplankton composition category it most closely resembled, to determine the appropriate conversion factor.

THE EASTROPAC AREA

The EASTROPAC area comprises the eastern tropical Pacific Ocean from 20°N to 20°S and from the American continent out to 120°W. The station lines on which LHPR profiles were obtained run north–south between 98 and 118°W, so as to form transects normal to the zonal current system (Fig. 1). Rather than group the profiles within rectangles based on latitude and longitude in the same way as Blackburn, Laurs, Owen and Zeitschel (1970), in their studies of the multiple correlation of biotic and abiotic variables in the horizontal plane, I have chosen instead to identify a series of oceanographic regions within the EASTROPAC area, each with consistent and definable characteristics, and the zooplankton profiles have been pooled accordingly.

Examination of all available station data, mostly as presented in the EASTROPAC atlases, indicated that there were seven such regimes characterized by the vertical variability of properties known to influence the vertical distribution of zooplankton. The areal extent of these regimes and the allocation of zooplankton profiles to them is indicated in Fig. 1; they have the following characteristics:

Region I. A triangular area bounded by the Mexican coast and by 10°N and 110°W, of variable currents, the surface water originating in the north from January to May after which, with the seasonal development of the north equatorial counter-current in Region III, the Costa Rica Current brings equatorial surface water inside California Current water which it entirely replaces in the area until August to October when a southerly component from the California Current again invades the area. Surface temperatures are higher here than in the rest of the EASTROPAC area, frequently exceeding 29°C from April to September; mixed layer depths are always moderate so that the bottom of the isothermal layer, of D1 (WYRTKI, 1964), lies between 20 and 50 m, the thermocline having a complex topography with much seasonal and areal variation. In the second half of the EASTROPAC year D1 was shoaler (20 m) and mixed layer temperatures warmer (28 to 29°C) than in February–March (50 m, 26 to 28°C), and northward coastal flow after June was associated with replacement of a thermocline ridge 300 to 400 miles off the coast by a trough, from which D1 shoaled towards the coast. This region overlies the greatest oxygen deficiencies in the North Pacific, and values below 0.25 ml l^{-1} occur within the oxygen mininal layer.

Region II. To the west and southwest of the first area the extension of the California Current as the north equatorial current dominates surface flow throughout the year; temperatures are lower, and vary more during the year than closer to the coast, from 21 to 26°C seasonally, with the effects of the northern hemisphere winter and of coastal upwelling at Baja California. The oxygen minimum tends to have slightly higher minimal values (0.25 to 0.50 ml l^{-1}) than in Region I, and the mixed layer tends to be deeper, so that D1 is typically greater than 50 m.

Region III. The north equatorial counter-current traverses the northern part of the study area between 5 and 10°N except between February and May, when it does not extend east of about 120°W at the surface, though it is detectable in the thermocline topography farther east at this time. The occurrence of this flow from the west is indicated in the slope of the thermocline downwards towards the south, from a zonal ridge at 10 to 12°N along the northern boundary of the current to a zonal trough centered at about 4°N, which indicates its southern boundary. Thus, D1 varies from 90 m in the south to only 20 m in the north, and there is considerably greater variation in its depth during any one cruise than there is between seasonal means. Profiles were obtained from the north equatorial counter-current, however, only in the second half of the year and these showed D1 to be much shoaler than in Region I north of the thermocline ridge at 10 to 12°N. The oxygen minimal layer includes values no lower than 0.5 ml l^{-1}, and ranges from 300 to 500 m in thickness.

Region IV. About 2° north and south of the equator the water column is very strongly influenced by seasonal equatorial Ekman divergence and by the shallow, eastward-flowing equatorial under-current; the latter lies close to the surface, its core being scarcely deeper than 50 m, and its latitudinal extent and relative velocity indicated by the equatorial troughing of isotherms in the lower part of the thermocline (12 to 20°C, Fig. 2) and by the location there of a salinity core (34.9 to 35.2‰).

Equatorial divergence causes the thermocline to approach the surface so closely that the mixed layer may be extremely shoal, commonly less than

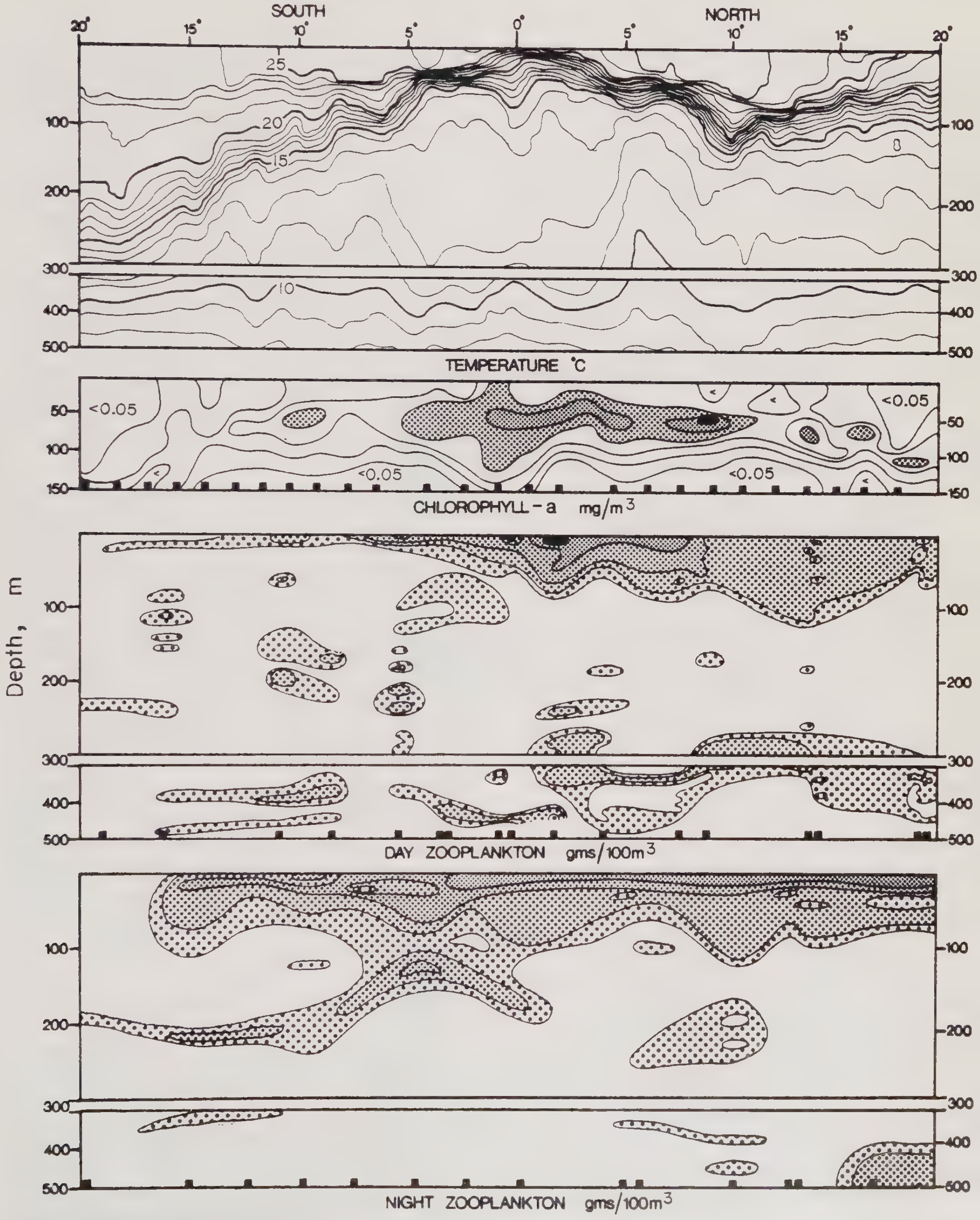

Fig. 2. Sections along EASTROPAC transects at 110°W; the symbols along the baselines indicate station positions. Chlorophyll-*a* is contoured at seven levels, from > 0.4 to < 0.05 mg m^{-3}; zooplankton at six levels, from > 2000 to < 100 g (100 m^3)$^{-1}$.

10 m deep. From May until about November this process appears to surface the equatorial undercurrent (CROMWELL, MONTGOMERY and STROUP, 1954; JONES, 1969) so that the permanent tropical mixed layer is obliterated, probably assisted by turbulent diffusion (WILLIAMS and GIBSON, 1974), resulting in a deeper homogeneous layer (⩽ 40 m), though at considerably lower temperatures (⩽ 20°C) than earlier in the year. This situation was established at some stations in June and July, 1967 (cruise 30) and remained so throughout the rest of the year; at all Region IV stations in December (cruise 60) the primary thermocline had been eliminated and a cool mixed layer (22°C) of rather variable depth was established. By February 1968 (cruise 76) the tropical mixed layer was re-established, though it was everywhere very shoal.

Consequent upon the general shoaling of the isotherms at the equator, the O_2 minimum layer, which has minimum values greater than 0.50 ml l^{-1}, lies very shoal.

Region V. Throughout the year, equatorial surface water is transported westwards by the south equatorial current broadly over the EASTROPAC area south of about 9°N and it is within this westward zonal drift that Region IV outlined above is embedded as a very narrow equatorial ribbon.

Region V is recognized as the region of strongest zonal flow of the south equatorial current, its northern extent limited by the southern boundary of the north equatorial counter-current at the 4°N thermocline trough or by a broad zone of convergence at 7 to 9°N when the north equatorial counter-current is absent. South of the equator, the permanent thermocline deepens southwards throughout the EASTROPAC region. An interruption in this slope by a region in which southward shoaling of the summer thermocline occurs is associated with a weak, subsurface south equatorial counter-current (TSUCHIYA, 1974); the southern edge of this current, where the mixed layer deepens again southwards, is taken as the limit of Region V.

This region has a mixed layer with relatively strong small-scale thermal layering at many stations both north and south of the equatorial divergence, this being especially true of those with a deeper D1. Variations in thermocline depth appear to contain no seasonal component and to be due to the relative instability of the upper 100 m here compared, in particular, with Region I.

Region VI. From about 7 to 9°S, the velocity of the south equatorial current slackens, the surface water mass changes its characteristics, and a summer thermocline occurs; this is a regime of gentle westward drift, increasing mixed layer depths and increasingly high values in the O_2 minimum towards the south. A number of distributions of planktonic animals and bathypelagic fish (AHLSTROM, 1971; MCGOWAN, 1971) appear to coincide with the boundary between Regions V and VI.

Region VII. In the extreme south of the area, from about 15 to 16°S, the south Pacific central water mass is evident in the water column, being principally indicated by a salinity maximum which progressively strengths and deepens towards the south, though the separation from Region VI is not very well defined. D1 increases progressively southwards, as does the summer mixed layer above it, and reaches 250 m at 20°S. Thermocline gradients are slight and only exceptionally is there no mixed layer temperature stratification, even above the summer thermocline. There are very low standing crops of all biota, and deepening of features of the phytoplankton profile, especially south of 14°S where the chlorophyll-*a* maximum occurs deeper than 200 m at some stations; oxygen values lower than 1.0 ml l^{-1} do not normally occur in the water column.

GENERAL FEATURES OF THE ZOOPLANKTON PROFILES

Zooplankton profiles for biomass, total numbers of organisms and for all sorted categories were computer-generated for each station; examination of the general profiles for biomass and numbers immediately indicated a high degree of commonality among their general features, especially when the profiles were pooled regionally. Copepods, being more numerous in all profiles by factors varying between 7 and 10, together with chaetognaths and euphausiids, whose biomass is also very important, dominated the form of the profile for biomass and number of organisms.

Three main features (Figs. 3 and 4) can be seen in most profiles and are defined below: an *epiplankton*, a *planktostad*, and *discrete layers* within the planktostad.

From the surface down to depths ranging from 50 to 150 m in all except nine of the 86 profiles of biomass and total numbers there is a layer of abundant zooplankton having dry weight values ranging from 1 to 1000 mg m^{-3}, and with numbers of all organisms frequently as high as 900 m^{-3} and rarely below 100 m^{-3}. It is convenient to apply the term *epiplankton* to this layer, following Fowler (1898), Vinogradov (1968) and others.

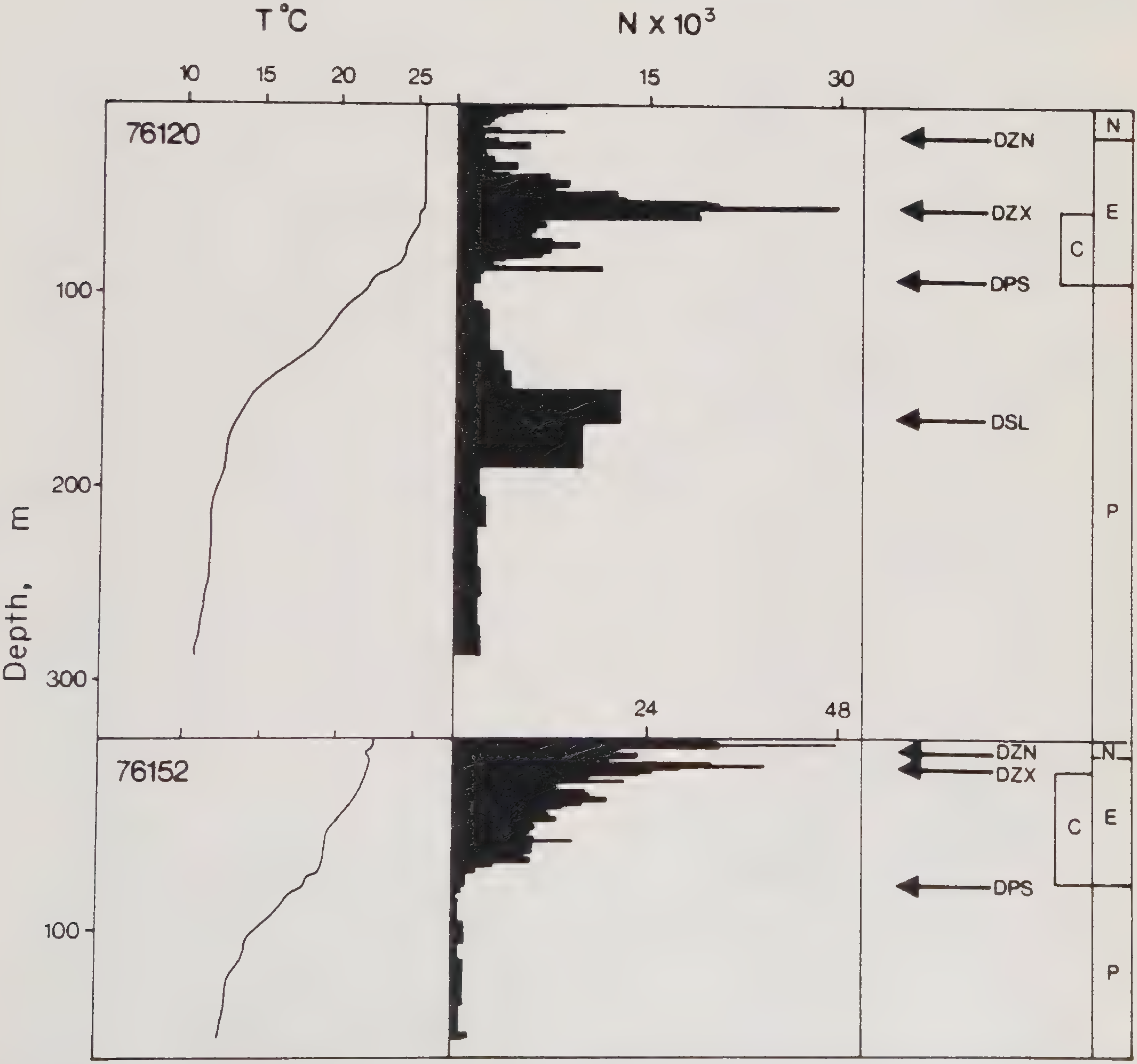

Fig. 3. Two exemplary shallow daytime profiles (total organisms 100 m^{-3}) to demonstrate their principal features; N = neuston, E = epiplankton, C = planktocline, P = planktostad. Remainder of notation as in text, p. 737.

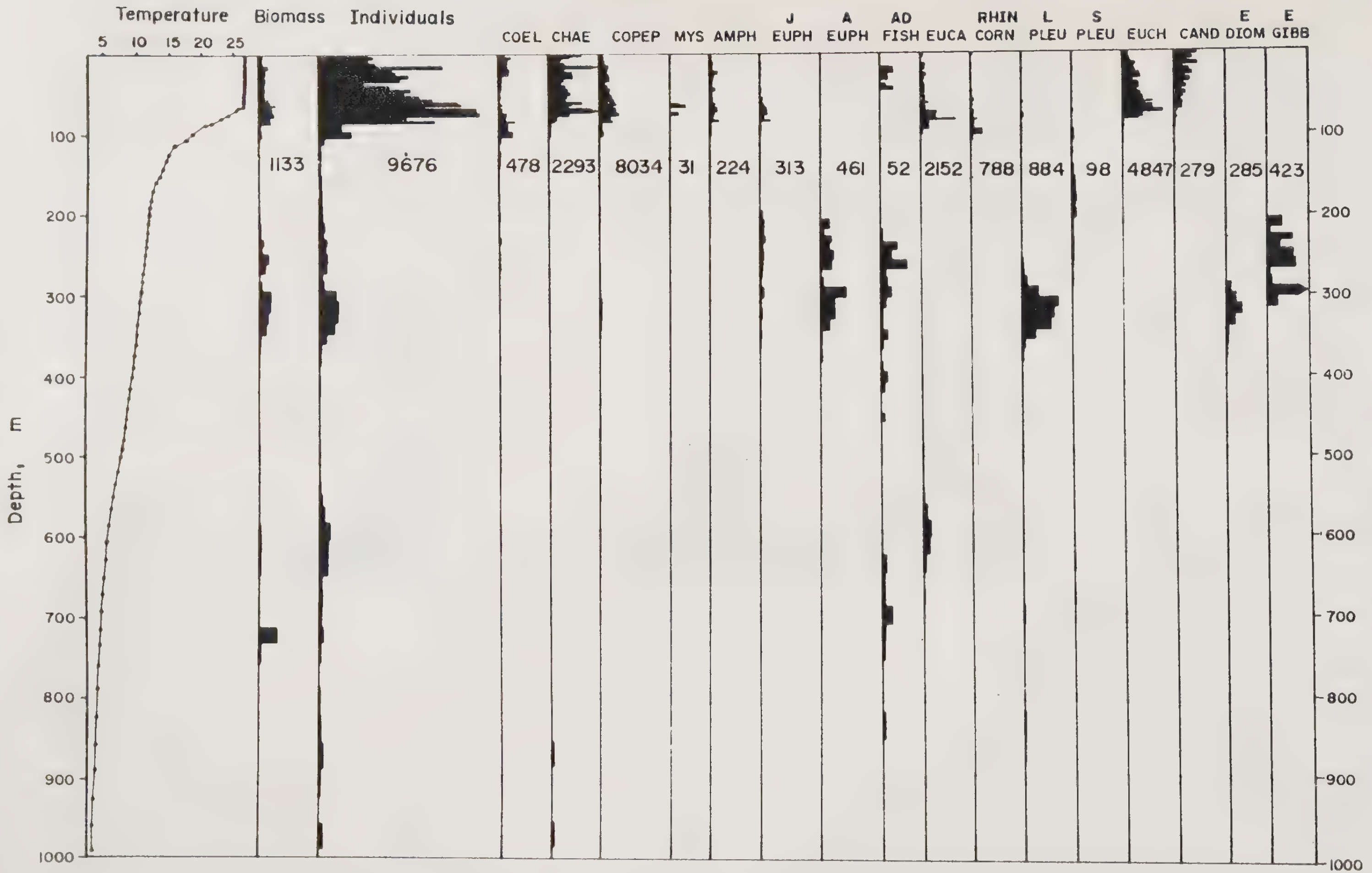

Fig. 4. Special deep daytime profile (76202) at 14°N to show layering of taxa; in this computer-derived plot the horizontal scales are arbitrary; against each histogram are indicated the maximum numbers per 100 m^3 or maximal biomass in g (100 m^3)$^{-1}$ reached in that profile. Abbreviations are of major and minor sorted categories, defined in text, p. 731.

The lower limit of the epiplankton is usually well defined at the bottom of a depth zone across which plankton abundance usually decreases by 100 to 1000 organisms m^{-3} per meter of depth increase, or about 2 to 10% of the epiplankton average value per meter and which can conveniently be described as a *planktocline*;* in day profiles a *zooplankton minimum* frequently lies at 10 to 25 m separating a layer of more abundant near-surface zooplankton from the main body of the epiplankton below. A major faunistic boundary occurs at the bottom of the epiplankton, which forms the lower limit for many species and genera of copepods, for all cladocera, for most polychaetes, and for some decapods.

Below the planktocline, plankton biomass and numbers are from one to several orders of magnitude lower (0.1 to 1.0 mg m^{-3} and *ca.* 10 individuals m^{-3}) and change very little with increasing depth to at least 1000 m. This can therefore be described as a *planktostad*,* which continues downwards for several thousand meters (e.g. VINOGRADOV, 1968: pp. 188 to 189), and within which rates of change are so small as to be unquantifiable in the present data.

Single interzonal species or groups of species occur both within the epiplankton by night and the planktostad by day, but are more prominent within the latter, where they form important discrete layers; these may, or may not, coincide with *deep scattering layers* (DSL), they extend throughout the sampled depth range of the planktostad, and they usually represent daytime populations of diel vertical migrants, or upper interzonal species in the sense of VINOGRADOV (1968, p. 51).

The biomass of such depth-discrete layers may approach 5 mg m^{-3}, and may be greater than the planktostad background by at least an order of magnitude, and also they may be extremely thin (5 to 10 m is not unusual) in the vertical sense. Such layers have previously been reported in LHPR profiles in the California Current (LONGHURST, 1967), the North Sea (KINZER, 1970), the North Pacific (BARRACLOUGH, LEBRASSEUR and KENNEDY, 1969) and the North Atlantic (Williams, personal communication) and, from our general knowledge of the oceanic distributions of DSLs, are probably a common feature in many parts of the ocean.

From examinations of the profiles of biomass and of total individuals, depths were assigned to the major features of the profiles; in almost every case the two profiles agreed but, when they did not, the data derived from the biomass profile were discarded:

DPS —depth of the bottom of the epiplankton, defined by the planktocline–planktostad boundary.

DZX—depth of the subsurface zooplankton maximum that may occur within the epiplankton.

DZN—depth of the subsurface zooplankton minimum that frequently separates the main body of the epiplankton from a near-surface layer, having its own maximum abundance within 10 to 15 m of the surface.

In addition, from the temperature record made by LHPR for each profile and from associated EASTROPAC station data, the depths of a number of related environmental parameters were determined:

D1 —the depth of the base of the mixed layer, from STD casts;

D2 —the depth of the base of the thermocline (WYRTKI, 1964), also from STD casts;

DE —the depth of the bottom of the euphotic zone, at the 1% incident light level, determined from Secchi disc extinction depths by appropriate conversions (LOVE, 1971);

DCLX—the depth at which the subsurface chlorophyll-*a* maximum occurs (YENTSCH, 1965), determined from Lexan bottle casts (LOVE, 1971);

DCX —the depth at which the maximal rate of uptake of 14-C was measured in

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*The general suffixes—cline and stad—used in oceanography to denote the presence or the absence, respectively, of a gradient (as in *thermo-*, *halo-*, *pycno-*, *oxy-*, etc.) are here used for the same purpose, as a matter of convenience, in relation to plankton.

simulated *in situ* primary production experiments (Love, 1971);

DPHX—the depth of the subsurface maximum of phaeopigment concentration, from the same bottle samples as used for chlorophyll-*a* determination.

Finally, though not used subsequently in the formal correlation programme, information was extracted on:

DCLN—the depth of the bottom of the major chlorophyll-*a* maximum where values fell to below a value of 0.05 mg m^{-3};

DON, DNOX—respectively, the depths of the oxygen minimal layer, and of the shallow NO_2 maximum, determined from reversing bottle casts.

The 19 sets of profiles of specially sorted taxa were then examined and depths derived for major layers (or for maximum abundance in unlayered taxa) both within the planktostad and the epiplankton (Table 1). In the case of diel migrant taxa, separation was made between depths of the main migratory parts of the population and the depths of the residual, non-migrating layers which are a characteristic feature of such taxa (e.g. Longhurst, 1967).

The data derived from the general profiles were stratified by time (day/night), season (cruise) and regionally, and an analysis of variance between the strata was performed, as was a linear regression in all unstratified permutations of two of the eight variables (Table 2). A stratified table of differences

Table 1. *Mean depths of variables, stratified by region;* $\bar{X}$ D–N *is the mean difference between day and night depths.*

	Zooplankton			*Phytoplankton*			*Environment*			
Region	DPS	DZX	DCX	DCLX	DCLN	DPHX	D1	D2	DE	DNO2
I	98.2	39.0	25.0	49.5	107.0	83.9	47.8	119.7	65.6	70.4
II	82.5	41.3	30.0	70.0	105.0	95.0	47.5	120.0	84.3	-
III	89.4	31.1	29.3	49.4	112.0	75.0	30.9	93.6	86.1	64.2
IV	77.6	11.9	22.9	38.4	108.0	66.6	25.2	98.9	56.8	51.6
V	89.0	25.7	31.5	52.8	122.0	76.8	36.1	113.3	64.3	58.9
VI	80.0	60.7	22.1	58.6	130.0	96.4	51.6	195.0	56.3	111.4
VII	-	35.0	39.2	120.8	150.0	146.7	68.3	251.7	77.2	-
$\bar{X}$	88.5 (±2.3)	30.8 (±3.2)	27.6 (±1.3)	55.3 (±1.7)	119.0 (±2.8)	84.0 (±3.0)	37.9 (±1.6)	126.6 (±4.1)	66.7 (±1.6)	71.3 (±3.1)
$\bar{X}$ D-N	+7.7	+10.4	-	+3.5	-	-6.0	+12.1	+4.7	-	-

Table 2. *Correlation coefficients* (r) *of linear regressions, all permutations of two of eight selected variables.*

	D1	D2	DE	DCLX	DCX	DPHX	DPS
D1							
D2	+.626***						
DE	+.161 NS	+.178 NS					
DCLX	+.555***	+.666***	+.413***				
DCX	+.209*	+.218*	+.444***	+.299**			
DPHX	+.115 NS	+.314**	+.057 NS	+.262*	-.045 NS		
DPS	+.338**	+.053 NS	+.204 NS	+.342**	+.286*	-.130 NS	
DZX	+.396***	+.415***	+.065 NS	+.294**	+.148 NS	+.066 NS	+.482***

NS—not significant ($P > 0.05$). *—just significant (P 0.01–0.05), **—significant (P 0.001–0.01). ***—very significant ($P < 0.001$).

Table 3. Depth differences (m) *stratified by time and region, between DZX, DPS and six environmental variables. Abbreviations as in text and Table 2. Stated significance is that between depths of indicated pairs of variables.*

	DAY		NIGHT		DAY + NIGHT
	I-III	IV, V	I-III	IV, V	I-VII
DZX = D1	+3 NS	-20 **	-6 NS	-3 NS	-5.0 ± 3.3 NS
= D2	-70 ***	-88 ***	-89 ***	-86 ***	-88.1 ± 4.5 ***
= DE	-29 ***	-40 ***	-47 ***	-43 ***	-35.4 ± 3.7 ***
= DCLX	-9 *	-28 ***	-21 ***	-26 ***	-20.5 ± 3.5 ***
= DCX	+18 **	-11 **	+2 NS	-7 NS	+3.4 ± 3.1 NS
= DPHX	-38 ***	-49 ***	-55 ***	-57 ***	-49.1 ± 4.4 ***
DPS = D1	+58 ***	+47 ***	+56 ***	+57 ***	+53.9 ± 2.5 ***
= D2	-15 **	+20 **	-24 **	-29 **	-25.8 ± 4.0 ***
= DE	+26 ***	+27 ***	+16 *	+19 *	+22.6 ± 2.5 ***
= DCLX	+47 ***	+38 ***	+41 ***	+37 ***	+40.0 ± 2.4 ***
= DCX	+69 ***	+56 ***	+63 ***	+55 ***	+61.1 ± 2.4 ***
= DPHX	+18 **	+17 *	+7 NS	+7 NS	+11.1 ± 4.0 **

(Table 3) between DPS and DZX and the other six variables was constructed and each difference subjected to analysis of variance and of significance.

These processed data were then used as the basis of an examination of the relationship between the variables and of possible reasons for the observed form of the zooplankton profiles.

VERTICAL EXTENT OF EPIPLANKTON

Preliminary examination of the general profiles showed that while the general features associated with the epiplankton could be recognized at nearly every station, there was great variability in detail, principally concerning the depth at which features occurred; it was also evident that the variability was rather strongly linked with the regional pooling of the stations. It is to be supposed that the planktocline, the depth at which the vertical extent of the abundant epiplankton is limited, would be the result of the presence of a constraint in the physical environment or by the insufficiency of the food supply below such depth; these possibilities are now explored.

Density and temperature

In tropical seas, temperature is a practical indicator of density of sufficient precision for present purposes and so we may define the pycnocline by D1 and D2, or as coincident with the thermocline.

Because of this relatively direct relationship between density and temperature, the lower part of the pycnocline coincided with the same groups of isotherms over the whole region; the data suggest that DPS and the 14°C isotherm coincide rather frequently, though this is most unlikely to be in any sense a depth-limiting factor in the distribution of the epiplankton, and the possibility was not investigated formally.

Analysis of the depth differences DPS-D1 and DPS-D2 showed that DPS usually occurred in the lower part of the pycnocline, and there was no case in which it occurred shoaler than D1, or within the mixed layer; in only 16 of the 75 profiles at which DPS could be identified did it occur deeper than D2. The mean depth differences were very significant in each case:

$$\mathrm{DPS} = \mathrm{D1} + 54 \pm 2.5\ \mathrm{m}\ (P < 0.001)$$
$$\mathrm{DPS} = \mathrm{D2} - 26 \pm 4.0\ \mathrm{m}\ (P < 0.001).$$

Significance at this level was maintained for all strata (time, season and region), and the linear regression DPS/D1 (D1 being the more satisfactorily determined parameter of the thermocline) showed significant covariance ($r = 0.338$; P 0.001 to 0.01) for all data strata.

An examination of the 16 exceptions showed that in 11 stations at which the epiplankton appeared to extend below the base of the thermocline (i.e. where DPS > D2), the difference was by a margin of only 2 to 17 m, possibly to be accounted for by the imprecision of the quantification of D2 from the temperature profiles.

As for the remaining exceptions, two stations (30215 and 60257) lay within the equatorial divergence cell in Region IV to the west of the Galapagos Islands where the thermocline had surfaced and D2 was relatively very shoal, at only 38 m in the case of 30215; two other stations (30246 and 60284) lay on the southern slope of the Costa Rica dome, having mixed layer depths less than 20 m and rather shoal values for D2 of $\lesssim$ 60 m (regional means were 92 to 117 m).

At the final station 76120, at which DPS apparently lay 101 m below D2, there was a deep migrating layer lying unusually shoal, and inseparable from the epiplankton, so DPS must have been calculated in error.

The eleven stations at which DPS could not be identified were, with a single exception, all at the extreme south of the EASTROPAC area where D1 and D2, but especially the latter, lie very deep (p. 734 and Table 1). In Regions VI and VII, DPS could be identified only at night stations in Region VI; at day stations in VI, and both day and night stations in VII, it was not possible to identify a planktocline below an abundant layer of epiplankton. These profiles suggest that in these regions of very deep pycnoclines it is only at night, as a result of the crepuscular rise of diel migrants that a planktocline is formed, and that even this does not occur south of about 15°S. Unfortunately, there were too few stations in Regions VI and VII to analyse statistically the relationship between DPS and density or temperature.

The single station (30233) in low latitudes at which DPS could not be identified was situated in an area of dynamic upwelling to the west of the Galapagos Islands, and no explanation for this anomaly is evident.

Light

EASTROPAC data on light penetration are derived from 30-cm Secchi disc extinction depths and therefore are available only for day stations. Reflecting the fact that the only important source of turbidity in this area is pelagic biological production, light penetration is closely correlated with the depth of the layer of abundant plant cells (Table 2). The mean value of DPS is deeper by 23 ± 2.5 m than DE ($P < 0.001$), and although the range of variability in this difference is not great, the attempt to demonstrate linear correlation fails ($r = 0.204$, $P > 0.05$), and it seems improbable that DPS is primarily determined by the light regime; even though DPS shows a very minor diel depth fluctuation, which has the correct sign to be caused by normal vertical migration patterns, the day–night difference (+ 7.7 m, Table 1) is not significantly different from zero ($P > 0.10$).

Oxygen

The eastern Pacific oxygen-deficient layer is shoal and very strongly developed in Region I, to the southwest of Baja California and the Mexican coast (BRANDHORST, 1959; WYRTKI, 1962). Earlier studies in this layer (LONGHURST, 1967) have shown that oxygen levels only below 0.2 ml l^{-1} may constrain the distribution of interzonal migrant zooplankton. This oxygen isopleth was as shoal as 75 m at some stations in Region I and at four of these (12006, 12030, 30250 and 30258) DPS was as much as 30 m deeper, and well into water with very high oxygen deficiency. Such observations suggest that oxygen plays a negligible role in determining the depth distribution of the epiplankton. Moreover, in most of the EASTROPAC profiles, the 0.2 ml l^{-1} isopleth lay much deeper than DPS.

Phytoplankton

Of the 86 LHPR stations, there were 77 at which profiles of chlorophyll-*a* and phaeopigments were also obtained and 48 daytime stations at which profiles of 14-C uptake rate were taken. These three parameters of the phytoplankton had a rather constant relationship: the subsurface chlorophyll maximum was underlain by a deeper phaeophytin maximum, while the depth of maximum gross production rate lay shoaler. At 11 southerly stations the phytoplankton sampling was not carried sufficiently far down to reach the chlorophyll maximum which lay very deep indeed (> 125 m) at some stations in Regions VI and VII.

Since the simplest hypothesis relating the depths of abundance of animals and plants is that zooplankton do not exist in abundance below the depth at which a significant standing stock of phytoplankton occurs the relations of DCLN with DPS were examined first.

DCLN lay between 105 and 115 m right across Regions I to V, showing remarkably little variance (Table 1): it did not appear to react to shoaling of D2 in very low latitudes in Region IV and deepened less strongly than D2 in the southernmost Regions VI and VII. Because of its relation with D2, therefore, DPS always lay shoaler than DCLN by 25 to 50 m in Regions II to VII; only in Region I, with its very well-defined and relatively shoal mixed layer, was there a closer correspondence between D2, DCLN and DPS. The lack of better correspondence between DPS and DCLN might indicate that an incorrect chlorophyll value was selected to define the latter; however, a value which would give a better match in Regions I to V (say the 0.1 mg m^{-3} isopleth) gives a rather poor match in the southernmost regimes, as would a value based upon a percentage of the maxmimal chlorophyll value.

As expected, the formal analysis of difference and correlation confirmed that DPS lay significantly deeper than DCLX and DCX:

$\text{DPS} = \text{DCLX} + 40\text{ m} \pm 2.4\text{ m } (P < 0.001)$

$\text{DPS} = \text{DCX} + 61\text{ m} \pm 2.4\text{ m } (P < 0.001)$,

and although the linear regressions indicate some covariance, this is not very significant (for DPS/DCLX, $r = 0.342$; P 0.001 to 0.01; for DPS/DCX, $r = 0.286$; P 0.01 to 0.05).

Taken together, the evidence on density, light, oxygen and phytoplankton indicates that the lower limit of the epiplankton is usually determined by the lower part of the thermocline, though not by its deepest isotherms and isopycnals, and that it occurs in a rather loose association with the lower limit of chlorophyll-rich water; it appears to be unrelated to light penetration or to oxygen content.

DEPTH CONTROL OF EPIPLANKTON MAXIMA

Within the epiplankton, DZX could be identified in 80 of the 86 profiles of biomass, of total numbers of organisms, of total copepods and of total chaetognaths. There is a greater diel variation in DZX than in DPS, and the regional mean day–night differences range from 6.8 (Region IV) to 45.0 m (Region VI), and because DZX is much shoaler than DPS, its day–night differences are a much higher percentage of its day depth, regional means ranging from 30 to 58%.

Diel variation in the depth of maximum plankton aggregation reflects two different processes: the nocturnal rise (or sinking) of the aggregated epiplankters forming the diurnal DZX, and the rise of interzonal species from the planktostad to their nocturnal layer depths within the epiplankton. A nocturnal deepening of DZX does not, therefore, necessarily imply nocturnal sinking of any individual plankters, for it may be due simply to the layering of interzonal species at night deeper than daytime DZX.

The preferential aggregation of zooplankters at any particular depth may be a response to a favourable feeding situation at that depth, or to their crowding against a barrier or constraint imposed by the physical or chemical environment. Though the first possibility seems *a priori* to be the more likely in the present profiles, both are now examined.

Constraint is only likely to be caused by density, because it has already been suggested that other possible contraints (light, oxygen) are inoperative even in the case of DPS which lies deeper, and so more under their possible influence than is DZX.

Density

The zooplankton maximum occurs very close to D1 in all strata, the overall mean value of CZX being 5 ± 3.3 m shoaler than D1; the difference DZX-D1 is not significantly different from zero ($P < 0.05$) for the whole data pool and for all separate strata with the single exception of daytime profiles in very low latitudes in Regions IV and V; some anomalously deep values for D1 in this area, especially where mixed layers are relatively difficult to interpret in the equatorial divergence cell, caused the mean difference for this stratum to be $\text{DZX} = \text{D1} - 20 \pm 5.6$ m. The linear regression DZX/D1 shows very significant covariance ($P < 0.001$). Thus, the layer of maximum zooplankton abundance within the epiplankton generally occurs some 50 m shoaler than DPS, and is very closely associated with the bottom of the mixed layer.

The aggregation of zooplankton at density discontinuities has recently been reported by

BOYD (1973) using an electronic particle counter, although the cause of the phenomenon remains obscure. Two possible explanations suggest themselves: firstly, that it may be a simple physical effect of the changed sinking rates to which any sinking particle will be subject at D1 or, secondly, it may be the result of an active food-seeking process. That the zooplankton profiles are not consistently skewed downwards towards DPS suggests that the physical process alone is not the cause.

Phytoplankton

The data show that zooplankton aggregation frequently occurs rather close to the depth of maximum 14-C uptake (DCX) and usually significantly shoaler than the depth of maximum chlorophyll-*a* standing stock (DCLX). In fact, the overall mean depths of zooplankton aggregation and maximum 14-C uptake are so similar ($DZX = DCX + 3 \pm 3.1$ m) that the difference between them is not significant ($P < 0.001$); correspondence is closer at night than by day, when marginally significant differences do exist. Surprisingly, the linear regression DZX/DCX is not significant (Table 2); this may be because the mean depth difference is so small, or because night data for DCX were derived from the nearest day station (p. 740). Because DZX and DCX coincide so closely, DZX lies above DCLX by about the same distance as does DCX: the mean difference is $DZX = DCLX - 20.5 \pm 3.5$ m ($P < 0.001$) and significant difference is maintained for all strata of the data (Table 3); furthermore, in this case the two variables show a high degree of positive correlation ($r = 0.294$, P 0.01 to 0.001).

This suggestion that zooplankters tend to aggregate in depths of actively dividing (high 14-C uptake) phytoplankton in preference to depths where less actively dividing (or low 14-C uptake) but more abundant phytoplankton occurs has important implications for the interpretation of the form of phytoplankton profiles to which we shall return later (p. 749); previous detailed correlations between animal and plant plankton profiles have suggested a rather different coincidence. ANDERSON, FROST and PETERSON (1972) and MULLIN and BROOKS (1972) have shown a correlation at three stations off Oregon and six off California, respectively, between maximum numbers of copepods and chlorophyll-*a* maxima in the mixed layer. HOBSON and LORENZEN (1972) at about 70 stations in the Gulf of Mexico, the Benguela Current and in the North Atlantic at 35 to 42°N, found a coincidence between chlorophyll-*a* maxima, microzooplankton (Lugols iodine samples) and pycnoclines. Unfortunately, neither of these sets of observations included 14-C uptake data, in the absence of which it is impossible to be sure that the conclusions reached would not have been different had all three sets of data been available.

In all EASTROPAC regions, the phaeopigment maximum (DPHX) was deeper than DCLX, as expected (e.g. YENTSCH, 1965; LORENZEN, 1967), by about 20 to 30 m so that its depth is much greater than that of DZX ($DZX = DPHX - 49 \pm 4.4$ m), the area of presumed highest rate of production of these pigments during the grazing process. It seems probable that the closer coincidence of DPHX with DPS, which is only slightly, though significantly, deeper is not functional and that both variables are likely to be independently related to the lower part of the pycnocline where sinking rates of both plant cells and faecal pellets will decrease.

Also occurring in close proximity in all regions to DPHX is the shallow NO_2 maximum (DNOX), an indicator of the depth of maximum remineralization of organic material by herbivores and heterotrophs (WADA and HATTORI, 1971); DNOX usually lay well below DZX (Table 1) and though within the depth range of the epiplankton is clearly unrelated to the depth of maximum zooplankton abundance but rather to the depth of aggregation of faecal material and senescent plant cells where microbial remineralization processes are most active.

These observations on the relations between DZX, density features and phytoplankton in the general zooplankton profiles can be, to a limited extent, extended by the data from the special sorting categories.

Of the six such categories which always occurred in their maximum abundance within the epiplankton (the genera *Euchaeta*, *Candacia*, *Acartia*, *Eucalanus*, *Lucifer* and *Stylocheiron*) only the last taxon showed important diel migration (mean 38 m). The nocturnal layer depth of *Stylocheiron* and the 24-h layer depths of the other taxa occurred very close to DZX and, thus, to DCX (Tables 1 and 4).

Despite this general coincidence with DCX there are individual deviations: the discrete layers of these six taxa lie with rather specific inter-relationships (Table 4). Thus, *Lucifer* lies in a relatively narrow layer (mean vertical range only 25 m by day), and shoaler (Table 4) than the copepods *Candacia*, *Euchaeta* and *Acartia* which lie closer to DZX; *Eucalanus* lies rather deeper (day mean 40 m) and *Stylocheiron* deeper yet (day mean 71 m). Since each of these taxa, with the probable exception of *Lucifer*, comprise several species, it has to be assumed that the epiplankton is composed of very many overlapping specific distributions, information upon which was not obtained from the samples though it was contained there: 21 profiles from EASTROPAC cruise 12 were analysed by Bruce Frost for six species of *Clausocalanus* (p. 731) and show how several co-occur at stations frequently and abundantly, but have specific layer depths and migration patterns. Three species (*C. parapergens*, *C. jobei* and *C. arcuicornis* occur in daytime in the planktostad and lower part of the planktocline (mean daily depths of maximum abundance 170, 79 and 85 m, respectively) but rise at night to different levels within the epiplankton (49, 54 and 40 m). On the other hand, *C. furcatus*, *C. minor* and *C. mastigophorus* occur in their greatest abundance very shoal in the day-

Table 4. Mean depths (m) *of the abundance maxima of the main layers of specially-sorted taxa, of the daytime vertical extent of these layers, of their range of vertical migration and of their residual layers for all regions combined.*

	LAYER DEPTHS				RESIDUAL LAYER DEPTHS	
	Day	Night	Extent	Range	Day	Night
EPIPLANKTON TAXA						
Eucalanus spp.	40	44	78	+4	-	-
Euchaeta spp.	28	17	50	-11	-	-
Candacia spp.	23	30	73	+4	-	-
Acartia spp.	23	10	84	-13	-	-
Lucifer spp.	19	17	42	-2	-	-
Stylocheiron spp.	71	33	56	-38	-	-
$\bar{x}$	34	25	63	-9	-	-
INTERZONAL TAXA						
Rhincalanus cornutus	229	19	178	-205	30	186
R. nasutus	300	30	74	-270	47	267
Pleuromamma gracilis	206	20	62	-186	40	257
P. abdominalis/xiphias	308	36	63	-272	30	100
Euphausia diomediae	322	16	59	-305	30	100
E. eximia	302	17	102	-285	22	100
E. gibboides	305	29	50	-276	70	120
Nematoscelis gracilis	283	57	22	-226	15	-
Nematobrachion flexipes	345	70	26	-275	17	110
Eucalanus bungii	301	[illegible]	56	[illegible]	-	-
$\bar{x}$	289	33	71	-255	33	156

time (12, 21 and 10 m) apparently sinking at night, the mean day–night difference being about 28 m.

Obviously, the nocturnal migration of interzonal species upwards into the epiplankton must cause a major shift in the vertical balance of biomass and numbers of individuals. To test this, progressive integrations were performed from the surface to 500 m, or to the bottom of the profiles if shoaler, for a number of the most important sorted categories: biomass, numbers of copepods, euphausiids, chaetognaths, pelagic fish, *Rhincalanus cornutus*, *R. nasutus*, large and small *Pleuromamma* species (mainly *P. xiphias*, *P. abdominalis* and *P. borealis*, *P. gracilis*, respectively). From these step-wise integrations it was possible to calculate the percentages of plankton above and below any given level, and hence the relative amount in the epiplankton. Table 5 shows that about 18% of the total biomass above 500 m was transferred from the planktostad to the epiplankton at night by migration of interzonal species.

Surprisingly, the copepod data show that less than 10% of all individuals down to 500 m participated in this translocation and added relatively small numbers to the very abundant small epiplanktonic species which, in all regions, comprised from 60 to 80% of all copepods above 500 m. The largest part of the nocturnal increase in epiplankton biomass is derived from migrant euphausiids and small mesopelagic fish, though these are much fewer in number.

Table 5. Percentages of certain categories of plankton above 500 m *which move into the epiplankton from the planktostad at night.*

Regions	I	III	IV	V	VI-VII
Biomass	[illegible]	[illegible]			
Total copepods	[illegible]	[illegible]	[illegible]		[illegible]
Juvenile euphausiids		[illegible]	[illegible]		[illegible]
Adult euphausiids		[illegible]	[illegible]	[illegible]	[illegible]
Chaetognaths	[illegible]	[illegible]			
Adult fish	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Rhincalanus cornutus	[illegible]			[illegible]	
R. nasutus	[illegible]			[illegible]	[illegible]
Pleuromamma (large species)	[illegible]		[illegible]	[illegible]	[illegible]
Pleuromamma (small species)	[illegible]	[illegible]	[illegible]	[illegible]	

Both juvenile euphausiids, in relation to adults, and small species of *Pleuromamma* in relation to large, show reduced contribution to the epiplankton at night, in addition to lying shoaler in their daytime residence layers within the planktostad. Of the groups examined in this way, chaetognaths show the least consistent pattern of nocturnal reinforcement of the epiplankton, the data indicating a more scattered dispersal.

Presence of near-surface maximum

In 38 of the 86 profiles, it was possible to identify a near-surface zooplankton maximum separated by a minimum from the main body of the epiplankton below (p. 737). The depth of this minimum (DZN) usually occurred between 10 and 20 m with a day–night difference (< 2 m) insignificantly different from zero.

There was variability in the frequency of occurrence of DZN both spatially and temporally. Most importantly, it was more frequent (50%) in daytime than at night (36%); this is evidently the effect of nocturnal shoaling of DZX and the consequent difficulty of separation of surface and subsurface maxima within the epiplankton.

In Regions I to III, where D1 is moderate, DZN was identified in the highest proportion of profiles, occurring in 22 (= 63%). Rather frequently in Regions IV and V, and especially at those stations most influenced by the equatorial divergence, the only maximum occurring within the epiplankton was very shoal and lacked the minimum above it: DZN was identified here in only 13 profiles (34%). This can best be interpreted as the result of the surfaceward displacement of DZX by the shoaling of the density parameters of the water column. In Regions VI and VII only three profiles (23%), none of which was in the gyral conditions of Region VII, included a subsurface minimum, presumably in response to the very great depths of the mixed layer and of DPS, and the very low plankton abundances, so that any aggregation within the epiplankton was hard to detect.

The chlorophyll-*a* profiles rather frequently (in 51 cases of the 86 examined) showed evidence of a secondary pigment maximum very close under the surface, generally no deeper than 10 m. In Regions IV and V, within the influence of the equatorial divergence and where a very high percentage of zooplankton profiles showed near-surface maxima, less than half of the profiles included such pigment maxima, perhaps indicating the grazing effects of 'surfaced' zooplankters.

LAYERING OF INTERZONAL SPECIES

The analysis of interzonal species was concerned with three components of the plankton: the deep, non-migrant taxa, the shoaler daytime layers of diel migrants, and the nocturnal layers within the epiplankton of diel migrants from the planktostad.

Layering within the planktostad

The layers of relatively abundant interzonal plankton that occur within the low-biomass water of the planktostad may form narrow strata only several tens of meters deep, or as rather thicker, more diffuse strata. The thin layers are distributed throughout sampled depths in the EASTROPAC material, while the thicker layers occur at rather constant depths and apparently in a rather constant relationship with sonic scattering layers. The upper and lower limits of the main layer at the 39 stations at which it was identified were from 226 to 330 m at daytime stations, and 227 to 349 m at a very few night-time stations: thus, in general, it extends for rather more than 100 m below a very consistent depth of about 225 m.

Both this main, thick layer of interzonal species and the bottom of the epiplankton can be correlated in about two-thirds of the daytime stations with the records from a 30-kHz echo-sounder which was operated continuously on high gain between stations. At each LHPR station the echogram was examined in detail, using the scale-expansion capabilities of the instrument to investigate the extent to which DPS, and the top (D′) and bottom (D″) of a layer of interzonal organisms could be recognized on the expanded echograms. This showed that there is a 70% probability that an echogram will predict DPS with a precision of ± 15 m, a 64% probability for D′ and a 52% probability for D″; that the probability decreases with depth of the feature predicted does not necessarily imply increasing layer-diffusion with depth, and is probably due to the effects of signal attenuation over longer sound-paths. It is reasonable to suppose that DPS and (at least) D′ were monitored in an approximate manner by the 30-kHz underway echograms taken throughout EASTROPAC and Fig. 5 shows echograms at 112 and 115°W in February to March 1967 which, compared with Fig. 4, considerably expand the description of the main features of the migrating layers within the planktostad.

Figure 5 shows that, while there is a good deal of small-scale variability in the depth of features within regions, there is remarkably little consistent variability between regions except at the southernmost end of the lines in Regions VI and VII, where the consistent deepening confirms the data shown in Fig. 2. The EASTROPAC data do not permit us to examine light levels at D′, which is considerably deeper (mean factor, × 3.3) than the depth of the euphotic zone though there is no simple correlation between these variables: many different species form the DSLs (see below) so perhaps a simple correlation is not to be expected.

However, DSL depths are well-known to be photo-regulated (e.g. BODEN and KAMPA, 1967) and light penetration in these oceanic areas where all turbidity is of biological origin (p. 740) is probably more uniform than most other variables in the water column which determine layer-depth.

Of the minor sorted categories of organisms, nine taxa (including seven single species), are interzonal diel migrants (Table 4); together with bathypelagic fish (principally the myctophid lanternfish *Diogenichthys* spp. and the gonostomatiid lightfish *Vinciguerria* spp.) these nine taxa comprise the bulk of the diel migrants in the samples.

As the table shows, most of the interzonal taxa had daytime layer depths, coincident with DSL depths, of between 250 and 300 m, and most layers were less than 100 m thick. The anomalous layer thickness shown for *Euphausia eximia* is largely influenced by a single station (76158) in the south equatorial current at which this species

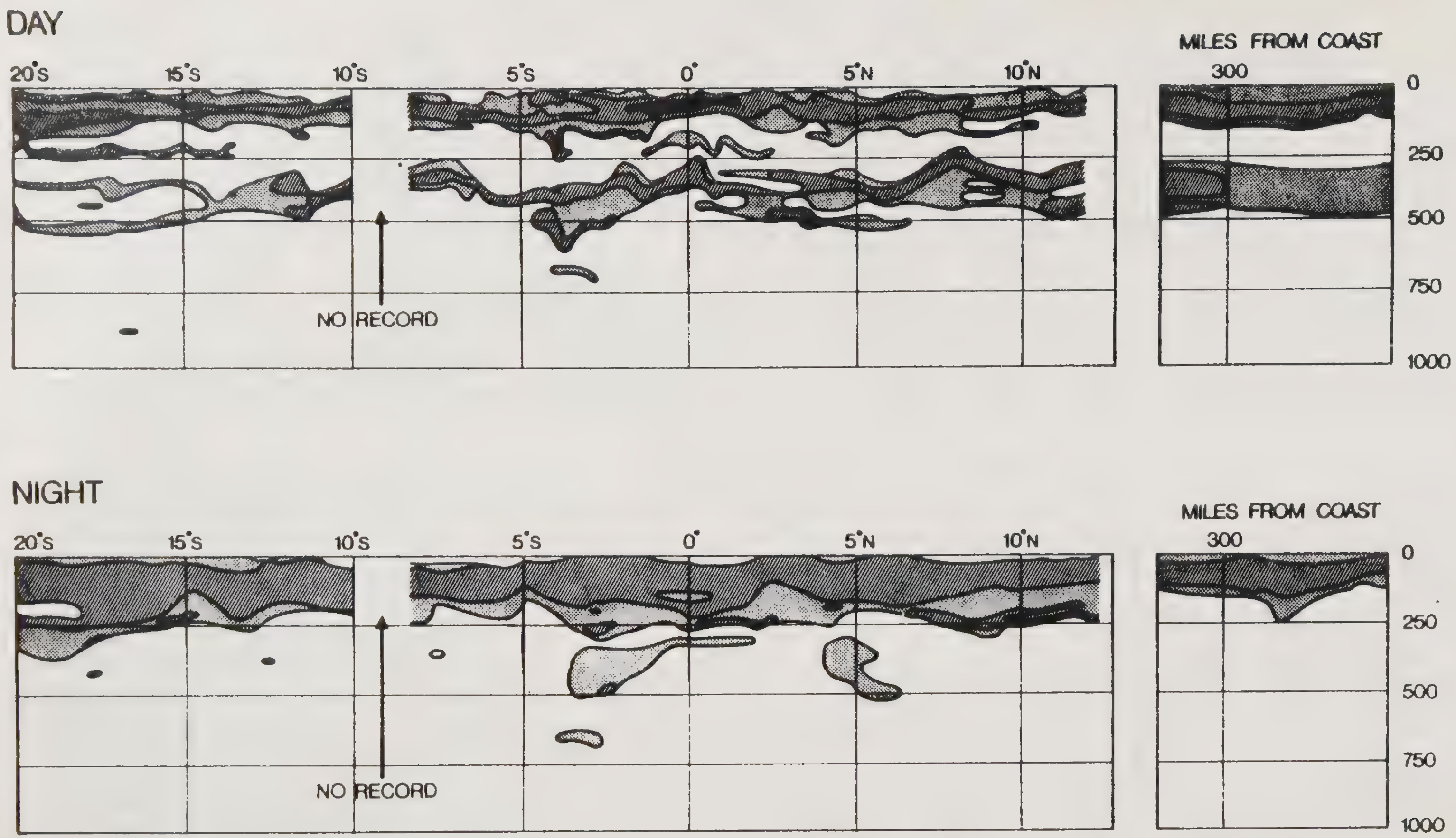


Fig.5. Sections of sonic scattering layers at 112°W and along a line from 12°N 112°W to the Mexican coast on the same scale. Contoured at 3 arbitrary levels of signal strength, in addition to 'no signal return'.

occurred in large numbers down to about 300 m without any layering.

As with the relatively non-migratory epiplankters, so the layer depths of the interzonal species do not coincide: *Euphausia eximia* and *Nematoscelis gracilis* regularly lie shoaler in the daytime than do the other species of euphausiids. *E. diomediae*, which generally lies deeper than any other euphausiid in daytime, also performs the greatest migrations and lies shoalest at night. PONOMAREVA (1963) confirms that this last euphausiid occurs very deep in the daytime in low precision opening–closing net hauls; she found maximal numbers at 200 to 500 m, but stragglers down to 1500 m.

The large species of *Pleuromamma* (*P. xiphias*, *P. abdominalis*) regularly lie deeper than the smaller species (*P. gracilis*, *P. borealis*), the latter occurring generally shoaler than 200 m; at night, however, the layer depths of the two groups of species are not so clearly separated. The large species of *Pleuromamma* were the most actively migrating copepods of the taxa examined in this study, occurring at night 250 to 300 m above their daytime levels.

Again, *Rhincalanus nasutus* and *R. cornutus* have mean daytime residence depths separated by about 75 m; compared with *Pleuromamma*, these are evidently much less consistent migrants, especially in the case of *R. cornutus*. Much more commonly than some other interzonal plankters, these species leave residual layers of individuals which fail to migrate both in the epiplankton in daytime and in the planktostad at night. ROE (1972a), indeed, found negligible diel migration in Atlantic forms of these two species off the Canary Islands in the SOND data, as did VINOGRADOV (1968) in all regions except in the tropical divergence that occurs at the boundary between north equatorial and equatorial counter-currents, where he found a distinct nocturnal shoaling of the population. Thus, the occurrence of residual layers of non-migrant individuals more commonly in these species than is the case for *Pleuromamma* occasions no surprise.

Two main regional phenomena can be detected in the data for layer depths within the planktostad and these are connected (1) with the thermocline shoaling at the equatorial divergence and (2) with the greater thermocline depth in the region of the southern summer thermocline.

Examination of individual station data shows that in the equatorial divergence in Region IV, the daytime layer depths of euphausiids remained generally deeper than 200 m at 8 stations, although at 10 others the daytime layers were shoaler than 50 m, even occurring in the upper 10 m; this occurrence of adult euphausiids at the surface was confirmed at several stations by actual observation (from the underwater ports of the bow-chamber) of red, adult euphausiids in large swarms. This was not an entirely passive reaction to water dynamics, for at each station not all euphausiids were surfaced, or normally deep; at 12100, for instance, *E. gibboides* remained centered at 320 m, while *E. diomediae*, *E. eximia*, *Nematoscelis gracilis* and *Nematobrachion flexipes* centered at 30 to 35 m. Similarly, among the copepods, at three of six stations in Region IV, both species of *Rhincalanus* and of *Pleuromamma* had layer depths at less than 30 m, mostly at less than 10 m, although at equatorial stations, part of the *Pleuromamma* population remained in daytime at depths exceeding 200 m.

In Regions VI and VII, to the south of the main stream of the south equatorial current, daytime layer depths of interzonal species as of the epiplankton, were greater than elsewhere in the survey. In almost every case, layer depths in VII were greater than in VI; at night, also, the tabulated data indicate that layer depths were deeper in these regions than elsewhere. These are the expected consequences of greater mixed layer depths and greater depths of features in the phytoplankton profile that have been discussed above, and are apparently unrelated to differential light penetration, which is remarkably slight (Table 1).

One interzonal taxon, *Eucalanus bungii*, which occurs deeper than all other sorted taxa, at depths in which black bathypelagic augaptalid copepods and scarlet hoplophorid carideans were beginning to occur in the sub-samples, does not appear to be a diel migrant; this species occurs extremely deep in only a few samples and forms discrete layers at depths ranging down to 860 m. The most prominent layers of this species occur in the special deep samples (76197, 76202, 76158) in which strong layers occurred at 600 to 860 m, each being itself less than 100 m thick. This species shows indication neither of vertical migration, nor of equatorial shoaling, and clearly plays an unimportant role in the tropical pelagic ecosystem, yet *E. bungii* is a very important and abundant interzonal plankter in the northern North Pacific where it lies generally below 200 m and shows little diel migration (VINOGRADOV, 1968); in the California Current (LONGHURST, 1967) it is widespread below 300 m and evidently it is even further submerged in the EASTROPAC area through which it becomes progressively less frequent southwards (station occurrences: Regions I to III = 34%. IV and V = 27%. VI and VII = 15%).

Nocturnal layers within the epiplankton

We have seen earlier (p. 741) that the layer of general plankton aggregation (DZX) lies very close to DCX and 20 to 30 m shoaler than the depth of the chlorophyll maximum; the data in Table 4 show that the depths to which individual taxa of interzonal migrants rise at night also correspond more closely to DCX than to DCLX. Thus, although the numbers of animals which participate in the diel translocation between the planktostad and the epiplankton are not relatively great (p. 743), they do contribute to the general observed aggregation around DZX.

The migrant interzonal taxa for which data were acquired have mean nocturnal layer depths which range from 16 to 70 m (Table 4); only two species, *Nematoscelis gracilis* (mean 57 m) and *Nematobrachion flexipes* (mean 70 m) differ more than 12 m from mean DCX, and five species had their maximum abundances with 10 m of DCX at night.

As within the planktostad by day, so there is specific variation between layer depths of the interzonal taxa within the epiplankton at night; among the four copepod taxa, those which lay deepest in the planktostad during the daytime (*Rhincalanus nasutus*, *Pleuromamma abdominalis-xiphias*) lay deepest in the epiplankton at night. The five species of euphausiids did not follow such a simple pattern, however, and the shoalest in the daytime (*Nematoscelis gracilis*) lay deepest at night. The most abundant euphausiid in the EASTROPAC area, *Euphausia diomediae*, regularly lay very shoal at night, having maximum abundances at less than 25 m in all regions.

ROE (1972b) showed quite clearly from the SOND data for six species of *Pleuromamma* that the larger species lay deeper than the smaller during the daytime and his Fig. 8 shows some indication that the small species also lie relatively shoaler at night, but the EASTROPAC data reviewed here suggest that lack of vertical resolution in the SOND samples (only five levels to 250 m) may have obscured the fine detail that evidently occurs within the upper 50 m at night.

CONCLUSIONS

The principal conclusions to be drawn from this study can be stated quite simply: zooplankton abundance is highest above the lower pycnocline and high biomass values rarely extend deeper than the layer of abundant chlorophyll; within this layer, both by day and by night, zooplankton tends to aggregate closer to the depth of maximum carbon fixation than to the depth of maximum chlorophyll standing stock. Finally, and perhaps less importantly, the presence of a near-surface enrichment of both animals and plants appears to have two possible causes: (i) extreme shoaling of the pycnocline which is associated with the shifting of biological processes close towards the surface, and (ii) an extremely stable mixed layer of moderate depth allowing the development within its upper few meters of a specialized neuston based on plant production processes which are probably to an extent isolated from those below.

Although several theoretical models which account for the general form of phytoplankton profiles have been published, these without exception include zooplankton grazing pressure as a constant, usually throughout the water column modelled. This could hardly be otherwise, for only very few and very recent studies have investigated zooplankton–phytoplankton vertical relations in detail.

The model of STEELE and YENTSCH (1960) to account for the vertical distribution of chlorophyll, based on those of RILEY, STOMMEL and BUMPUS (1949), explains the observed chlorophyll distribution by the sinking of plant cells; accumulation of cells is assumed to occur either in response to density discontinuities or to the decreased sinking rates of plant cells below the euphotic zone due to their changing physiology in the absence of light.

These models recognize two conditions: the very shallow chlorophyll maximum which occurs when a phytoplankton population is increasing exponentially, and a deeper chlorophyll maximum when the phytoplankton population reaches an approximately steady state, later in the summer in high latitudes. In the former case, the chlorophyll and gross photosynthesis maxima coincide; in the latter, the chlorophyll maximum occurs deeper than the photosynthesis maximum.

As BLACKBURN, LAURS, OWEN and ZEITSCHEL (1970) showed, EASTROPAC standing stocks of phytoplankton, zooplankton, micronekton and fish varied seasonally by a factor of less than two, a very small variability relative to high latitudes; moreover, except in the eastern EASTROPAC area, where no LHPR hauls were taken, and the seasonal cycle is strongest, there was no detectable lag between the seasonal maxima of phytoplankton and zooplankton. Blackburn's study, which is based on the most comprehensive time-series of data available for the low-latitude pelagic ecosystem, thus confirms the previous prediction of HEINRICH (1962) that producers and consumers of plant material should co-vary seasonally in the open tropical ocean. It further suggests that here one cannot expect to find the detailed coincidence in the vertical sense between maxima of chlorophyll-*a* and carbon fixation rate which can exist ephemerally in higher latitudes with greater instability in the seasonal production cycle. Thus the EASTROPAC profiles might generally be expected to approximate the summer chlorophyll profiles of much higher latitudes, and the sections presented in the EASTROPAC atlases (LOVE, 1971) confirm that this is the case.

What is new in the LHPR profiles is the demonstration that zooplankton aggregation, and hence grazing pressure on plant cells, is strikingly non-uniform with respect to depth and concentrates closer to the depth of maximal plant production than to maximal plant material. It is hard to avoid the suggestion, therefore, that a causal relationship exists between the form of the profiles of herbivore and producers. That, in short, the form of the chlorophyll profile is influenced, or even determined, by a depth-differential in the grazing pressure of herbivores, in addition to the effects of differential sinking rates invoked in the earlier models.

Of course, not all the zooplankters profiled in this study were, in fact, obligate herbivores, nor did they comprise all the pelagic herbivores present in the water column. However, the numerical profiles are dominated by small copepods which are at most only one trophic level above the primary herbivores whose biomass is likely to be dominated by very small organisms, and hence it is reasonable to consider the plankton profiles studied here as dominated by herbivorous organisms. There is evidence that levels of maximum abundance of the microzooplankton, which in this region must be extremely important consumers of primary production, coincides at EASTROPAC stations with DZX as determined in this study (e.g. BEERS and STEWART, 1971). It seems unlikely that the larger organisms of the micronekton (BLACKBURN, LAURS, OWEN and ZEITSCHEL, 1970) contribute importantly to herbivore grazing pressure, so it seems reasonable to equate LHPR-plankton in this region with herbivore distribution.

An hypothesis similar to that put forward here has already been proposed by LORENZEN (1967) on the basis of a small number of LHPR stations, at which phytoplankton profiles were also obtained, off Baja California. Further. VENRICK, MCGOWAN and MANTYLA (1973) have suggested that differential zooplankton grazing from animals concentrated above the chlorophyll maximum layer in low latitudes may help to maintain a sharp gradient above it, but propose that the deep chlorophyll maximum is ultimately determined by the nutrient regime. Such suggestions are an advance on the earlier models discussed above which depend on decreased sinking rates of plant cells, but the hypothesis has yet to be tested directly to validate the relationship which could be demonstrated in the EASTROPAC data only in a statistical sense; direct validation depends on simultaneous and matched high precision profiles not only of plant pigments and zooplankton but also of plant production rates. So far as I am aware, production profiles of the required precision have not yet been made.

The grazing hypothesis also raises the question of why additional grazing pressure does not develop deeper than DZX, where the chlorophyll profile suggests that food availability for grazing organisms is higher than at DCX. Why do the interzonal herbivores traverse the chlorophyll maximum in their nocturnal rise (p. 742), to seek depths where phytoplankton biomass is apparently always lower?

Two possible answers suggest themselves: firstly, that the phytoplankton population at the chlorophyll-*a* maximum is physiologically and biochemically less attractive as a food source than the plant cells at the depths of maximum gross photosynthesis or, secondly, that the other factors presumed to determine the rate and extent of diel migration, and of residence depth of non-migrants—light and temperature—over-ride the selection of the depth of maximum chlorophyll.

Certainly, the plant cells in the photosynthesis maximum (DCX) differ biochemically from those deeper (e.g. JEFFREY, 1974) and actively dividing cell populations will contain a higher proportion of larger pre-division cells which have been shown to induce increased feeding rates in a calanoid copepod (RICHMAN and ROGERS, 1969); the deeper cells are senescent, may not be actively dividing, and may be less attractive to herbivorous plankton. On the other hand, one must be impressed by the rigidity of migrant plankters' response to light intensity (e.g. BODEN and KAMPA, 1967; BACKUS, CLARKE and WING, 1965) which simply may not permit sufficient flexibility of response for zooplankton grazing pressure to develop on plant cell concentrations at whatever depth these may be encountered.

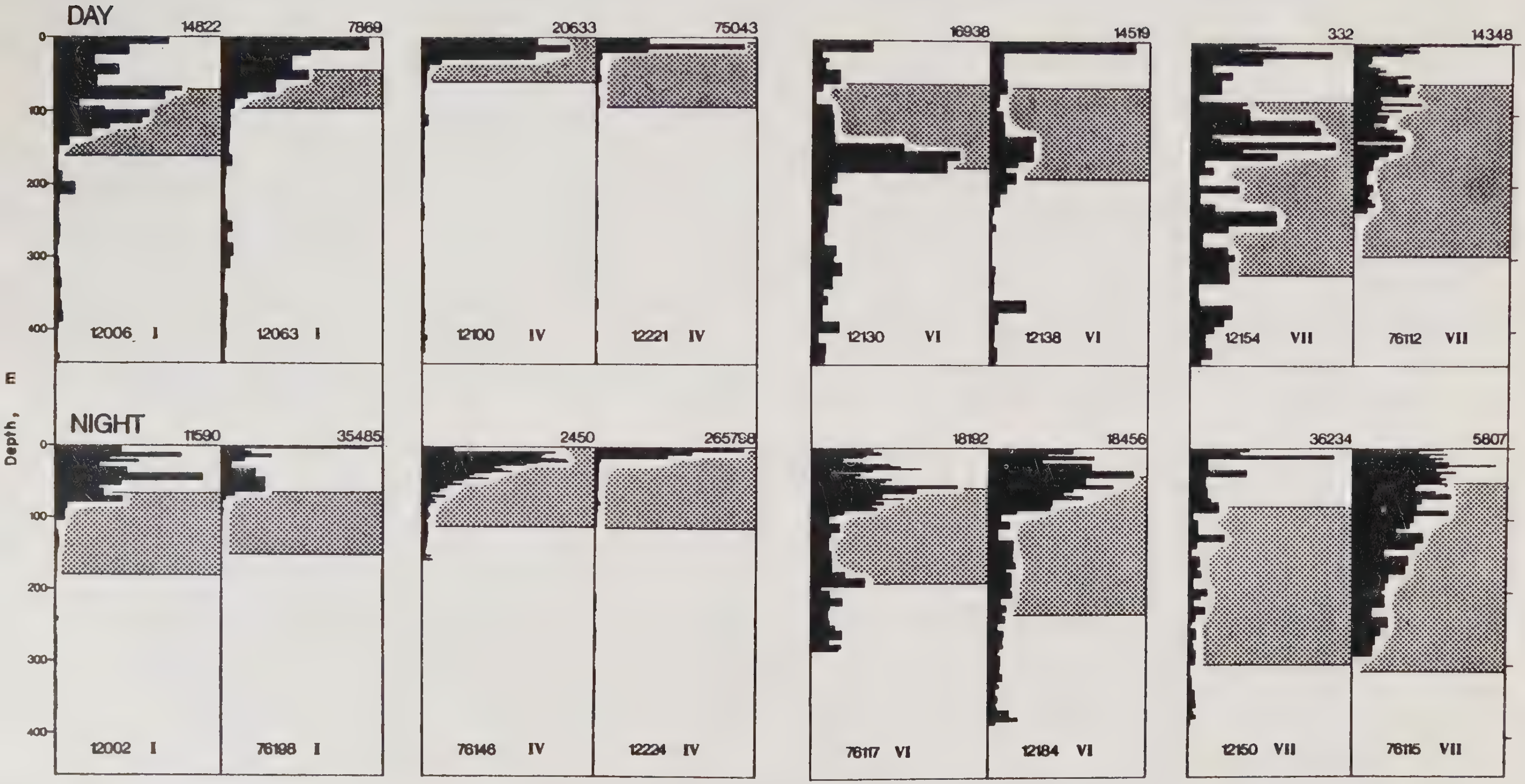
The general hypothesis that there is a relationship between the nature of zooplankton profiles and the vertical distribution of density and phytoplankton production is now examined in the light of regional and seasonal differences within the EASTROPAC area.

It is in Region I that plankton profiles (Fig. 6) most frequently show all major characteristics of the epiplankton, and this is clearly related to the isothermal mixed layer defined by an extremely sharp thermocline. In general, D1 is here sufficiently deep for the development within the mixed layer of a sub-surface zooplankton maximum separated from a surface maximum and this is associated with the development of characteristic phytoplankton profiles.

As expected, DZX shoaled in the second half of the year to about half its mean depth for February to March but, despite this crowding surfaceward by the shoaling of D1, the zooplankton profiles retained their typical form; very high zooplankton volumes occurred near 100°W in cruises 30 and 60 in relation to doming off Costa Rica. Even though tunicates and coelenterates were unusually abundant in these profiles (especially 30254) their essential profile-form remained typical of the region.

Only four stations were occupied in the north equatorial current in Region II, one in February to March 1967 and three in the December to January following: these are insufficient to characterize the plankton profiles in this region, but give no evidence of being significantly different from those characteristics of Region I.

Because of its seasonal occurrence in the study area (p. 732) profiles were obtained from the north equatorial counter-current (Region III) only in the second half of the year and these showed D1 to be much shoaler than in Region I to the north of the thermocline ridge marking the northern boundary of the north equatorial counter-current. Related to this, the zooplankton profiles frequently showed no separation between surface and subsurface maxima within the



ig. 6. Two exemplary profiles for each of four regions (I, IV, VI and VII) by day and by night, to show main characters of typical profiles of these regions; the thermocline, as indicated by depth interval between D1 and D2, is stippled. Maximal numbers of organisms (100 m^3)$^{-1}$ are indicated above each profile.

epiplankton, and mean DPS was shoaler than in Region I.

In the second half of the year in Region IV the very strong vertical eddying as the equatorial under-current surfaced resulted in a relatively cold and deep mixed layer, which was reflected in the distribution of the main features of the epiplankton; however, early in the year when D1 is less than 10 m, the epiplankton extends relatively deeper into the thermocline than in regions with moderate depths of D1 (Fig. 6). The ratio DPS/D1 for Regions I, II, III and V ranged from 1.7 to 3.8 for all seasons; in Region IV, however, it was 3.5 in June to July when the thermocline was deepest, but reached 9.6 in December to January and 45.8 in February to March when the thermocline was shoalest. This confirms that in extreme conditions of shoal thermoclines, the apparent lower limiting depth of the epiplankton responds principally to some factor other than density, for which there is no discontinuity at D2; the difference in depth between DZX and DCX remains relatively slight at all seasons in this region despite the important variations in D1, suggesting that under these very unusual conditions the link between plants and animals is greater than that between either and density.

Values for D1 in Region VI are intermediate between those in Regions I to III and V to the north and the greater depths in VII to the south, and the decreased mixed layer stability in VI implied by the step-wise temperature profiles above D1 is apparently reflected in the zooplankton profiles which here mostly do not include a subsurface minimum (Fig. 6); the existence of a depth zone of relatively sparse plankton in the upper part of the epiplankton is evidently a characteristic of regions with a thermostad above D1. Most profiles in Region VI have a simple subsurface maximum within the epiplankton or else a relatively complex system of maxima which are usually rather obviously correlated with density features (Fig. 6). The profiles of chlorophyll-*a* and carbon fixation are not sufficiently detailed, however, to demonstrate similar correlations with density.

To the south of 14°S, in the gyre proper where south Pacific central water characteristics occur, stations were worked in Region VII only in February to March, in the southern summer. These zooplankton profiles (Fig. 6) are mostly unlike those at any other stations in the EASTROPAC area; daytime profiles from 8 to 14°S have a very shoal surface maximum and several discrete subsurface maxima, commonly at depths exceeding 100 m, while in the southern gyral water the profiles were composed of almost uniformly low zooplankton densities from the surface to the greatest depths sampled. At night from 8 to 14°S, nocturnal migration upwards resulted at several stations in relatively heavy plankton densities from the surface to a planktocline at less than 100 m depth.

Because neither DZX nor DCX could be as well defined as in more northerly regions, and because DCLX was apparently often located deeper than chlorophyll sampling was carried, the relationship between plant and animal profiles appeared to be relatively loose here. This may well be a result which is more apparent than real, however, and to some extent is certain to be a reflection of the inadequacy of the standard EASTROPAC sampling protocol under these conditions.

This analysis of the EASTROPAC data suggests a generalization which may be extrapolated to other areas of the ocean: in fact, to wherever the phytoplankton profile includes a chlorophyll maximum which underlies a primary production maximum. VENRICK, McGOWAN and MANTYLA (1973) review deep (< 100 m) chlorophyll maxima in the Indian Ocean, the Sargasso Sea, the Gulf of Mexico and the northwest Pacific, and their own data show that one extends from 80°W to 180°E and from 45°N to 25°S in the Pacific Ocean. The EASTROPAC data suggest that the chlorophyll maximum is usually overlain by the depth of the maximum rate of primary production, itself probably corresponding to the depth of maximum photosynthetic rate per unit of chlorophyll (ICHIMURA, 1956).

In higher latitudes this pattern occurs only for a few weeks or months each summer, as STEELE and YENTSCH (1960) have suggested and as ANDERSON, FROST and PETERSON (1969) have shown off Oregon at about 45°N. In areas of strong divergence or coastal upwelling it cannot be expected to occur at all, as is seen in the EASTROPAC profiles off South American (LOVE, 1971), and in the Somali Current profiles published by YENTSCH (1965). Not only does the instability of the water column in such places preclude the establishment of the relationship postulated here, but also strong seasonal vertical migration occurs in the zooplankton. As in high latitudes, where the zooplankton profile in winter is quite different from those observed in the present study due to deep over-wintering populations of sub-adult copepods (e.g. VINOGRADOV, 1968), in intermittent low-latitude upwelling situations the same may occur in the interstadial (LONGHURST, 1967). Under such circumstances the vertical distribution of grazing pressure must be quite different from that in stable water columns in the EASTROPAC area.

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AN ACOUSTIC METHOD FOR THE HIGH-SEAS ASSESSMENT OF MIGRATING SALMON[1]

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ABSTRACT

A system of free-floating acoustic buoys with upward-looking transducers has been developed for use in assessing high-seas salmon stocks. The transducers, operating at 120 kHz, are suspended 46 m below the surface. The fish counts and the range to each fish are obtained in digital form, and the data are radioed from each buoy to the tending vessel where the data are decoded and recorded on magnetic tape. The present system consists of four buoys although the receiver-decoder system can accommodate up to 10 buoys operating synchronously.

The assessment of fish stocks is of obvious importance to all segments of the fishing industry in planning their respective operations. A problem of particular interest to the United States Section of the International North Pacific Fisheries Commission has been the assessment of immature sockeye salmon, *Oncorhynchus nerka*, which occur in abundance each summer south of the central Aleutian Islands in the North Pacific Ocean. It has been found (Hartt 1962, 1966) that immature sockeye salmon, mainly of Bristol Bay origin, migrate westward through this area in summer and that their relative abundance is related to the number of mature fish returning to Bristol Bay the following year (Fisheries Research Institute Staff 1960; Rogers 1972, 1973, 1974). This information has been used since 1960 as a means of forecasting the Bristol Bay run. Because the size of the run may vary by a factor of 10, an accurate forecast with a lead time of nearly a year is of obvious importance to the fishing and canning segments of the industry. Mathews (1966) has shown, by means of a comprehensive model simulating the cannery portion of the fishery, the relative value of run forecasts of varying precision. Run forecasts are also of value to the fishery management agencies in setting preliminary escapement goals and in planning their early season strategies to meet these anticipated goals.

The assessment of immature fish at Adak Island has been done by the Fisheries Research Institute using a fine-mesh purse seine 400 fathoms (730 m) long at a series of stations from 5 to 50 nautical miles off the southern shore of Adak Island. From 1956 through 1967, no station pattern was followed—purse seine sets were made randomly, mainly in an area within 20 nautical miles of shore. Since 1968, the fishing has been conducted uniformly at five stations spaced at approximately 10 nautical mile intervals between 5 and 50 nautical miles offshore.

Although the purse seine is a useful tool for providing information on abundance, species composition, and age composition of the stocks present, it suffers from several disadvantages as a research tool. Its use is limited to periods of moderate sea conditions resulting in significant gaps in the time-space coverage in this particularly stormy region. A maximum of five sets can be made in a day under ideal conditions which yields only 2½ h of actual fishing. Also, seines give no direct information on depth stratification or schooling of the fish, and in areas where the direction of migration of the fish is not uniform, multiple sets are required to sample all of the stocks present. Variability in direction of migration is not a serious problem in the area south of the central Aleutian Islands because the direction of migration of immature salmon is uniformly westward (Hartt in press). In an effort to overcome the sampling limitations of the purse seine, the Fisheries Research Institute and the Applied Physics Laboratory jointly developed an

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acoustic assessment system that can be used alone or in conjunction with the purse seine. Some of the anticipated advantages of such a system were that it could obtain abundance estimates and swimming depths with around-the-clock operation in a wide range of weather conditions.

PRELIMINARY CONSIDERATIONS

The final configuration of the system was determined, to a large extent, by consideration of problems related to obtaining adequate numbers of representative samples. The preliminary indications were that most of the fish of interest were concentrated near the surface at a depth of 10 m or less. This conclusion was based on the results of experiments in which longline and gill net gear were fished at various depths (Manzer 1964; Machidori 1966; French et al. 1967) and also by direct visual observation of salmon in the purse seines. This concentration of fish near the surface precluded the use of a hull-mounted device since such a system would necessarily exclude the top 3 or 4 m of the water column. This led to consideration of a transducer suspended in some manner below the main body of fish.

A transducer mounted on a towed platform with a coaxial cable to the towing vessel was considered initially but was abandoned because of the anticipated difficulty of developing a platform that could maintain depth and attitude stability while maintaining position to the side of the vessel. Since the extreme water depths precluded an anchored system the approach eventually adopted was to suspend the transducers from free-floating surface buoys with self-contained electronics. Consideration of the anticipated sampling statistics indicated the need for a multibuoy system which in turn suggested radio telemetry of the data from the buoys to a central shipboard receiver and recorder. This is the type of system that was eventually constructed.

The sampling statistics of particular relevance to the design and operation of the buoy system concerned: a) the level of effort required to obtain a specified precision in the estimation of the density of the fish and b) the purse seine effort required to obtain comparable precision in the estimation of the species composition of the population.

Extensive purse seining over a period of several years indicated that the salmon were relatively sparse and probably did not school or otherwise interact to a significant degree. Under these conditions the echo counts may be assumed to have a Poisson distribution with a parameter, μ, that is proportional to the number density[5] of the fish. Thus we have,

$$\mu = \rho_0 V_s \qquad (1)$$

where V_s is the sampling volume of a single counter and ρ_0 is the average fish density defined so that μ is the expected number of echoes per acoustic pulse. If we assume large sample theory, the minimum number of acoustic pulses required to be $100\alpha\%$ confident that the relative error of the estimate of ρ_0 does not exceed ϵ is given by,

$$M_{\min} = \frac{d_\alpha^{\,2}}{\epsilon^2 \rho_0 V_s} \qquad (2)$$

where d_α is the $100\alpha\%$ point (two-sided) of $N(0,1)$. The crucial feature of Equation (2) is that the sampling effort must be increased as either ρ_0 or V_s decrease. Preliminary estimates of ρ_0 based on purse seine data, while quite crude, indicated that V_s should be as large as possible subject only to the tradeoffs necessary to obtain an adequate signal to noise ratio. Also, the need for multiple buoys sampling mutually disjoint volumes was indicated.

The high-seas salmon population generally consists of a mixture of species so that it is necessary to determine species composition by some means. In the area south of the central Aleutians significant numbers of chum salmon, *O. keta*, occur mixed with immature sockeye salmon during the sampling period, and occasionally pink, *O. gorbuscha*; coho, *O. kisutch*; and chinook salmon, *O. tshawytscha*, are present in small numbers. The only nonsalmonid species generally found in this area, at the depths being sampled, is the Atka mackerel, *Pleurogrammus monopterygius*. This species generally occurs in small numbers relative to the salmon so that, if counted, it will not seriously affect the estimates of the density of the salmon. Further, this species does not have a swim bladder so that by the proper choice of the detection threshold level these fish will not be detected by the sonar.

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[5] For echo counting the number density is the quantity of interest. If acoustic echo integration is utilized, the density on a mass basis is appropriate.

Species and age discrimination by acoustic means is not currently possible so that it is necessary to obtain samples by purse seine in order to determine the species and age composition of the population.

Since sockeye salmon is the only species of interest, we may treat the purse seine samples as binomial events in which the parameter of interest is the proportion, p, of sockeye salmon present in the population. If asymptotic normality is again assumed, it is found that the sample size required to be $100\alpha\%$ confident that the relative error of the estimate of p will not exceed δ is given by,

$$n = \frac{(1 - p)\, d_\alpha^2}{p\, \delta} \tag{3}$$

where d_α is that defined for Equation (2).

Equations (2) and (3), as indicated, provide information on the sampling necessary to achieve prescribed levels of precision in the population estimates. A direct but somewhat crude comparison of the purse seine and the acoustic buoys may be made on an area basis. The purse seine has a nominal length of 400 fathoms or about 732 m. The area swept out in a round haul[6] is about 42,600 m². For a transducer having a beam width of 28° to the 3 dB points and suspended 46 m below the surface, the area ensonified is approximately 390 m². Thus the purse seine sweeps out an area about 110 times as great as the area ensonified by a single acoustic pulse. The pulse interval is approximately 10 s. However, it has been found that the individual fish remain in the pattern for longer periods of time, typically about 30 s, although a precise estimate is not available at this time. Thus, a single buoy would have to operate for at least 1 h to obtain coverage equivalent to a single round haul. The additional coverage obtained using 30-min tow hauls is not known precisely but the limited data available indicate a factor of two or three over the round hauls. Thus, to provide coverage comparable to that of the purse seine a single buoy would have to operate for a minimum of 3 h. A comparable sampling time is obtained using Equation (2) with $\rho_0 V_s$ estimated using a typical seine haul of 150 fish. The seine hauls may vary from zero to well over 1,000 fish from which it follows that the time required for adequate acoustic samples may vary, inversely, by corresponding amounts. The sampling considerations just outlined played a significant part in the choice of the hardware configuration and the decision to utilize multiple buoys.

SYSTEM DESIGN AND CHARACTERISTICS

Figure 1 is a schematic illustration of the high-seas assessment system showing only a single buoy. In operation up to 10 buoys can be deployed, each sending information to the shipboard decoding and recording system. A four-buoy system has been used at Adak to help assess the migrating salmon population. A simplified block diagram of the buoy system is given in Figure 2, and a photograph of the buoy is shown in Figure 3. The buoy and shipboard system are discussed below.

The buoy contains an acoustic system which gathers fish count and depth distribution data, a logic system which processes and provides temporary storage for these data, and a telemetry system which sends data to the monitoring ship. The acoustic system operates at 120 kHz and samples the population every 10 s. Sample rates can be changed to 5-s or 2.5-s intervals if desired. The system transmits a 200-μs pulse (24 cycles at 120 kHz) at a source level of + 106 dB. Target returns must be greater than a preset threshold (approximately 2 V) for at least 100 μs before they are validated. This technique, and an adequate source level to give a worst case[7] signal-to-noise ratio of 10 dB, minimizes false target counts.

Pulse elongation and amplitude testing techniques are used to automatically adjust "end-of-sample" so that surface returns and near surface bubbles are not counted.

Measurements at the University of Washington and at Adak during summer operation have shown that the "average" target size of the migrating salmon is about −30 dB within the aspect angles encountered in the sample volume.

A typical plot of signal return versus aspect angle from a single fish is shown in Figure 4. This polar diagram shows target strength from the

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[6] Purse seining is normally done in a standard manner using tow hauls in which the seine is held open in a semicircle for 30 min before closing and pursing. In a round haul the seine is set in a circle and pursed immediately after closing the circle.

[7] The worst-case condition exists for minimum target strength (−45 dB) at maximum range (46 m) at the −3 dB point in the transducer beam pattern.

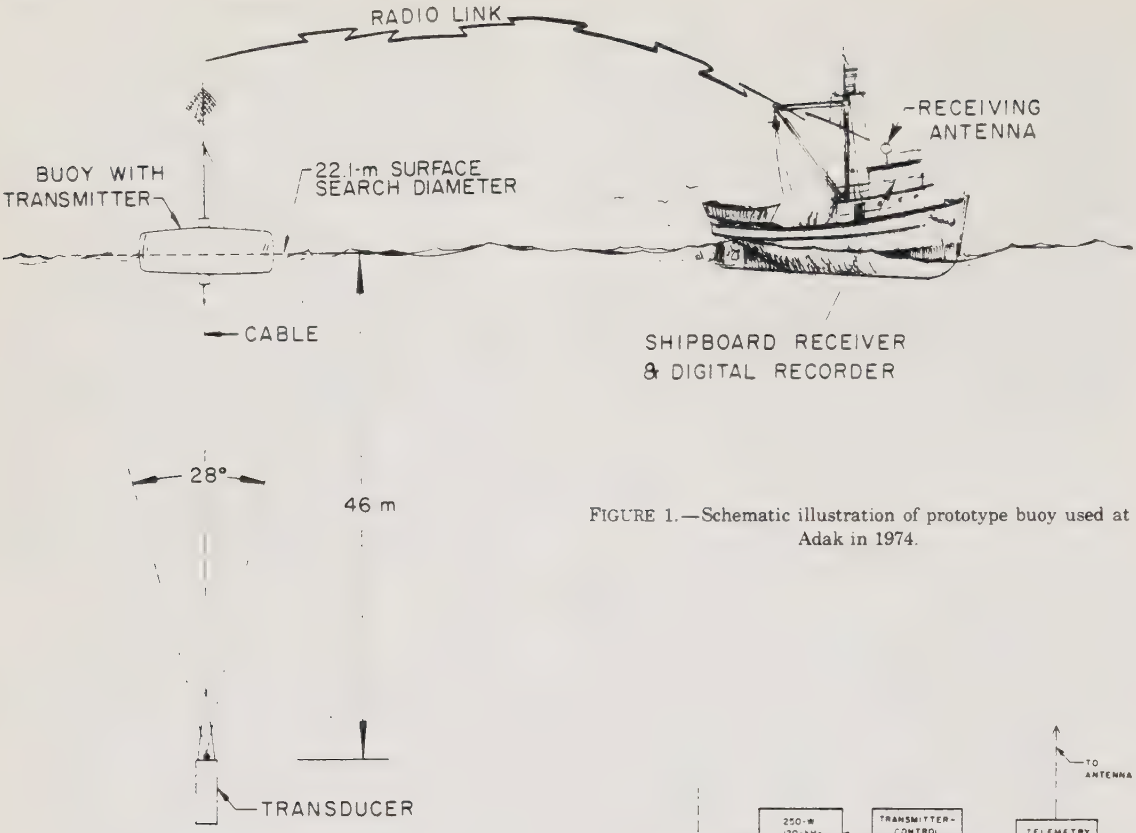
RADIO LINK
RECEIVING ANTENNA
BUOY WITH TRANSMITTER
22.1-m SURFACE SEARCH DIAMETER
CABLE
SHIPBOARD RECEIVER & DIGITAL RECORDER
28°
46 m
TRANSDUCER

FIGURE 1.—Schematic illustration of prototype buoy used at Adak in 1974.

ventral, head, dorsal, and tail aspects. Inspection of this figure shows that the target strength decreases rapidly for head or tail views but is fairly constant at −30 dB over ±30° when viewed from the dorsal or ventral aspect. This severe dependence of target strength on aspect angle was the limiting factor in the choice of transducer beam width. For the high-seas system, a 28° conical beam is used. This gives an adequate sample volume and minimizes target-size fluctuations to a manageable level. A time-variable-gain (TVG) receiver, adjusted so that its output for a particular target is independent of target range, is used to limit signal dynamic range at the detector. This technique, and proper adjustment of absolute sensitivity, keeps the search volume relatively constant over a fairly wide range of target strength (±15 dB).

Estimates of the fish density in the Adak area indicate that the average count per sample will be less than one fish. Schooling habits of these salmon also reveal that only rarely will more than a few salmon be included in any one sample.

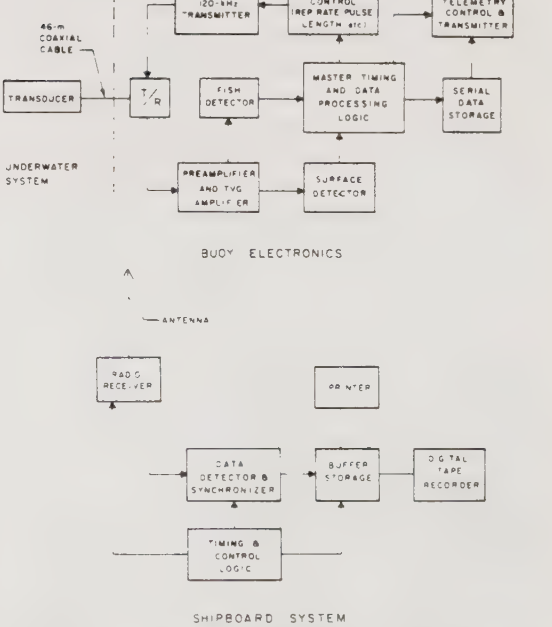
TO ANTENNA
250-W 120-kHz TRANSMITTER
TRANSMITTER-CONTROL (REP RATE PULSE LENGTH etc)
TELEMETRY CONTROL & TRANSMITTER
46-m COAXIAL CABLE
TRANSDUCER
T/R
FISH DETECTOR
MASTER TIMING AND DATA PROCESSING LOGIC
SERIAL DATA STORAGE
UNDERWATER SYSTEM
PREAMPLIFIER AND TVG AMPLIFIER
SURFACE DETECTOR
BUOY ELECTRONICS
ANTENNA
RADIO RECEIVER
PRINTER
DATA DETECTOR & SYNCHRONIZER
BUFFER STORAGE
DIGITAL TAPE RECORDER
TIMING & CONTROL LOGIC
SHIPBOARD SYSTEM

FIGURE 2.—Simplified block diagram of the prototype high-seas system.

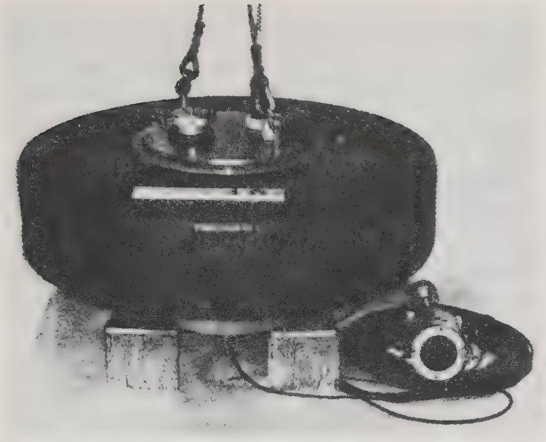

FIGURE 3.—Buoy deployed with detection and recovery gear.

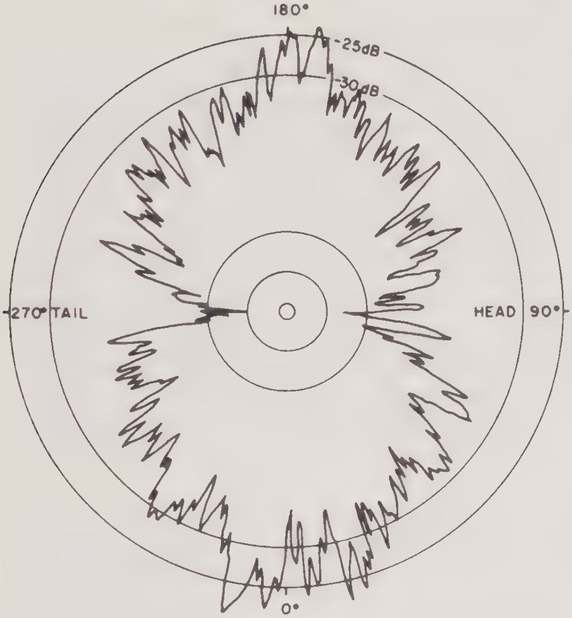

FIGURE 4.—Typical signal level as function of aspect angle for a single fish.

Storage was therefore limited to include data from a maximum of seven fish. The number of fish counted per sample and depth of each fish (to the nearest meter) are stored in a serial shift register memory, as are data on buoy identification and a data synchronization code. These data are stored in a format which makes telemetry noise and false counts easily recognizable and therefore easy to eliminate.

After all data from one acoustic pulse are gathered and stored they are automatically shifted through the telemetry system for transmission to the monitoring ship. Frequency-shift-keying (FSK) through the audio inputs of commercially available transceivers is currently used. The frequency response of the audio channels limits the bit rate to 100 Hz. A reliable telemetry range of 15 km in fairly rough seas has been achieved using this technique. A 6-MHz telemetry system has been developed which will increase the useful range to 100 km and will allow the use of radio direction finding equipment found aboard most seagoing vessels for buoy recovery.

In the current configuration, the buoys will operate continuously for 5 days before battery recharging is necessary. The acoustic and logic systems were carefully designed to minimize average power drain. COSMOS elements were used in logic design, and transmitter and receiver standby current is very low. Battery life is therefore limited by the telemetry system. The relatively low data rate requires that the transmitter be on for 0.6 s/sample. However, the redesigned telemetry system can increase data rate by an order of magnitude which will increase buoy life between charges to more than 6 wk.

The shipboard system consists of a telemetry receiver, a data synchronizer with buffer storage, a printer, and a digital tape recorder. Data from up to 10 buoys can be received and processed at the monitoring ship. Real time readout is provided by the printer. The digital tape recorder provides data storage for later computer analysis.

FIELD OPERATIONS AND RESULTS

The acoustic buoy system has been operated in the Adak area during the summers of 1972, 1973, and 1974. The 1972 operation suggested significant design changes in the electroacoustic portion of the system. These modifications were accomplished during the winter of 1972-73. The results of the 1973 operation indicated that special attention had to be given to system sensitivity and field calibration which was done prior to the start of the 1974 field season. The present configuration represents an essentially final design with only minor modifications to be made in the future.

Whenever feasible, the acoustic buoys have been operated at the same station and at the same time as the purse seine in order to obtain comparable data. This was not always possible, however, since it was more convenient to operate the buoys continuously for several hours whereas the seine vessel required only 2 h for a set after which it proceeded to the next station. Occasionally the buoys were operated at a station which had been fished by the seine on the same day but not at the same time. Also, even at the same station, it was not feasible to set the seine directly around the buoys so it cannot be said that the two gears sampled precisely the same water. This is of some significance in any gear comparison since there was considerable set-to-set variation in purse seine hauls made at the same station.

Buoy launch and recovery presented no difficulty in any weather conditions in which buoy operation was attempted. Buoy operation is usually limited by the presence of heavy breaking seas with whitecaps in which case the entrained air causes ambiguous echo counts. In the Adak area the limiting weather conditions for operation of either the purse seine or the acoustic buoys depend strongly on the wind direction. Generally the purse seine can be operated in winds up to a maximum of about 20 knots. The acoustic buoys have been operated in higher winds with no serious difficulty in launch or recovery. However, the aforementioned problem of entrained air usually limits buoy operation to winds of less than 25 knots. The buoys, however, can be operated continuously for longer periods of time since, once deployed, no further human activity is required except to monitor the digital printout.

The buoys operate synchronously so that the data for each acoustic pulse may be radioed to the tending vessel as soon as it is obtained. The echo count data are in digital form in which all of the data from each acoustic pulse is coded into a single 60-bit word for telemetry to the shipboard receiver. Each of these 60-bit words contains: a) buoy identification number, b) the number of echo counts up to a maximum of seven, and c) the range from the transducer to each of the targets. The data system requires that the indicated number of targets agrees with the number of ranges actually recorded and that the target ranges must form a nondecreasing sequence. This redundancy permits the detection and rejection of spurious or noise contaminated data. The binary coded 60-bit words are formatted to be compatible with the CDC-6400 computer[8] used for the data reduction. The tape reading and data processing can be accomplished using only FORTRAN and certain FORTRAN callable subroutines thus avoiding the necessity of machine language programming.

The range discrimination of the acoustic system is 25 cm, i.e., two fish separated in range from the transducer by 25 cm or more will be detected as individual fish. Six binary bits are allowed for each of the seven possible ranges. This presently corresponds to a range resolution of 1 m, i.e., more than one fish may be detected and recorded in a single 1-m range increment if they are physically separated in range by at least 25 cm. Target coincidence is a possibility, particularly if the fish are dense or tend to school. This has not been a problem in high-seas use since the average number of echoes per pulse has been of the order of one.

Figure 5 shows typical depth distribution histograms corrected for the effect of a conical sampling volume. The most striking feature is the shallow depth at which most of the fish are found, usually 5 m or less. This had been anticipated and illustrates the need for an upward-looking device.

There is the possibility of ambiguity in the interpretation of echoes originating very near the surface. Indeed this usually proves to be the limiting condition in the operation of the buoys. This situation manifests itself by the consistent presence of targets in two or more successive range increments below the surface. More detail

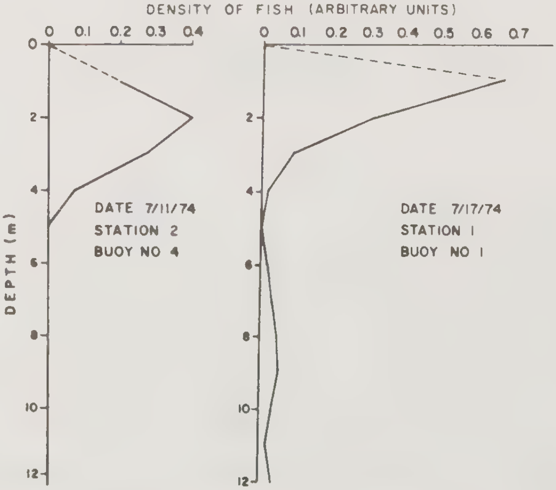

FIGURE 5.—Typical depth distribution histogram.

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[8] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

near the surface can be obtained by increasing the depth resolution to 0.5 m from the present 1 m. This increased depth resolution would necessitate the elimination of the first 14 m of the 46-m water column above the transducer since only six bits are available for each range word. This is a desirable tradeoff, however, in view of the concentration of the fish near the surface.

Figure 6 is a series of plots of the computed areal densities of the salmon obtained by integrating the depth distribution histograms over the depth. Also plotted are the purse seine catches which were obtained in reasonable time and space proximity to the buoys. The data are reasonably consistent although significant departures occasionally occur. There are several possible sources for the observed discrepancies: a) set-to-set variations in seine hauls, b) similar variations in the sonar counts, c) the inability of the purse seine and the acoustic buoys to sample precisely the same volumes of water, and d) possible attraction or avoidance of the acoustic gear by the fish. The variations within gear types can be explained by the "patchiness" of the salmon. The digital printouts tend to show small groups of fish, rarely giving more than three echo counts, occurring with widely varying interarrival times. This observation indicates the existence of relatively large areas that are nearly devoid of fish thus explaining the occasional twofold variations in successive seine hauls made at the same station.

Sonar gear avoidance or attraction by the fish is a potentially serious problem, the magnitude of which is not yet known. Occasional sea lions have been observed around the buoys but they usually departed after several minutes. Also, there is little evidence to indicate that the fish are attracted to the sonar gear since none of the observed targets remains in the ensonified region for more than a few pulses. Sonar gear avoidance is a more likely prospect. The Stellar sea lion is common in the area being sampled and it is a known predator of salmon. The sonar buoy is similar in size to that of a sea lion so that avoidance is a distinct possibility. Secchi disc readings of 15 m are typical so that the buoy or cable may be detected at significant distances by the fish. Day versus night data differ slightly but as yet there are too few data on which to base a conclusion concerning gear avoidance.

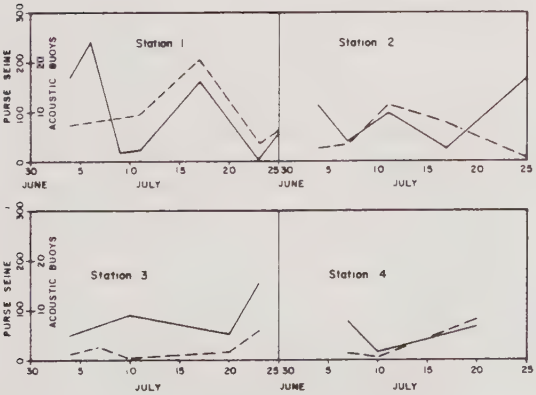

FIGURE 6.—Plots of computed relative areal densities (-----) and purse seine catches (—) by date and station for 1974.

All of the acoustic data from which Figure 6 was obtained were pooled and the sample correlation coefficient for the buoy-purse seine was computed. A value of 0.547 was obtained which, under the assumption of normality, is significant at approximately the 0.5% level (t distributed with $n - 2 = 19$ df). The results indicate that the acoustic buoys can obtain statistically significant population information as well as such ancillary information as depth distribution and density during both day and night. Additionally, indirect information on schooling is available by observing the interarrival times of the fish although this has not been investigated in detail.

The design of the acoustic buoy system is essentially fixed although modifications for use in other situations are possible. For example, a bottom anchored version for use in water depths of about 100 m has been designed but fabrication has not begun. Another possible design change is in the radio telemetry system. The present system, while reliable, is inefficient. An improved system has been designed and will be fabricated upon allocation of a suitable frequency by the Federal Communications Commission.

The current approximate unit cost per buoy, including the radio transmitter, is \$6,000. The shipboard receiver-decoder cost is approximately \$2,000. The tape recorder currently used is a Kennedy Model 1400 digital incremental which records at 556 bits/inch on ½-inch magnetic tape on 10-inch reels. It is "off the shelf" but is interfaced to the receiver-decoder. The interfacing cost is approximately \$1,000 which should remain constant for interfacing to any digital incremental recorder.

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MFR PAPER 1173

Southern California Recreational and Commercial Marine Fisheries

ALEC D. MacCALL, GARY D. STAUFFER, and JEAN-PAUL TROADEC

OVERVIEW

Southern California marine recreational and commercial fisheries exploit a large number of coastal fish species. An initial analysis of the current status of the more important stocks was undertaken in 1974. The results for northern anchovy, *Engraulis mordax*, California barracuda, *Sphyraena argentea*, Pacific bonito, *Sarda chiliensis*, jack mackerel, *Trachurus symmetricus*, white seabass, *Cynoscion nobilis*, and yellowtail, *Seriola dorsalis*, are documented in this report. Brief status reports for Pacific mackerel, *Scomber japonicus*, and Pacific sardine, *Sardinops caeruleus*, are included. These stocks are shared by various fleets fishing along the coast of southern California and the Pacific coast of Baja California. The U.S. partyboat fishery, in which fishermen rent space aboard a boat for a day or half day, has been popular in southern California since the 1920's (Young, 1969). In the last decade this fishery has caught about 4 million fish annually there. Fishing from private boats, shorelines, piers, and jetties is also very popular but statistics have not been routinely collected (Pinkas, Thomas, and Hanson, 1967 and Pinkas, Oliphant, and Haugen, 1968). A small round haul fleet supplies bait dealers with live anchovies for fishermen on partyboats and private boats to use as bait and chum.

The U.S. commercial fishery has two major components: a small purse seine fleet, which was once active in the sardine fishery and now harvests anchovies, jack mackerel, bonito, and tuna (Perrin and Noetzel, 1970) and market boats which use such gear as longlines and gill nets and supply the fresh and frozen fish market. Included in this report are discussions on the flexibility and trends in target species of the partyboat and purse seine fisheries, and analyses of anchovy fishery interactions and trophic relationships.

The tone of this investigation has been that of expedient fishery analysis, in which detail is sacrificed for speed, achieving maximum cost-effectiveness, and identifying areas where further investigation is needed and is likely to be fruitful. Originally this work was recommended at the State-Federal Marine Fisheries Research Program Planning Workshop held 12-15 March 1973 in San Clemente, Calif. (proceedings compiled by Squire, 1973).

This work should provide significant information for the formulation of positions and plans for regulatory agencies managing these resources. We have attempted to avoid making recommendations regarding the course of future exploitation of southern California fish resources except for the determination of approximate limits of sustainable yields and lower limits on age at first capture (Table 1). However, where resources are or appear to be exploited beyond maximum sustainable yield, reduction of catch and/or effort is strongly recommended.

The two California pelagic wetfish stocks showing very large standing biomasses, **northern anchovy** and **jack mackerel**, presently appear to be lightly exploited. Maximum sustainable yields of anchovy appear to be 10-20 times the present annual catch level of 130,000 tons, and jack mackerel should be able to sustain catches 4-8 times larger than the recent annual catch level of 55,000 tons. The "older" wetfish stocks—**Pacific sardine** and **Pacific mackerel**—are extremely depleted and show little likelihood of recovering to previous levels of abundance in the near future, even under the present fishing moratoria. Mexico is making large catches of these species; however, it is difficult to determine the proportion of catches coming from northern stocks relative to those coming from the southern stocks, or the Gulf of California.

The larger sport fish stocks are in various states of exploitation. The **yellowtail** resource appears to be lightly exploited, and has shown an apparent increase in availability to sport fishermen since the cessation of large-scale commercial fishing in 1954. The increase in availability may be due, in part, to more favorable ocean temperatures. Maximum sustainable yield (MSY) appears to be 3-6 thousand tons annually, with recent sport catches ranging from 0.5 to 2.0 thousand tons. As the sport catch appears to take a large fraction of the northward summer migration, it is unlikely that catches from California waters can be significantly increased.

White seabass appear to be somewhat depleted. Data from the commercial fleet operating in both Californian and Mexican waters indicate the species may be harvested at near maximum substainable levels. Catch per unit effort of white seabass from partyboats has declined over the last 2 decades, creating some uncertainty as to the true status of the stock. The white seabass

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Table 1.—Present state of exploitation and estimated potential of major recreational/commercial stocks.

		Estimated mean annual catch 10^3 short tons				Present major fishery segments (% 1970/72 total catch)					
Stock	Geographical range	1940-1949	1950-1959	1960-1969	1970-1973	U.S.-based sport	U.S. Comm.	Mexican Sport/Comm.	Potential yield 10^3 short tons	State of exploitation	Remarks
Northern anchovy	Southern California, northern Baja California	3	18	30	129	5 (bait)	.55	40	[1]1,500-2,000	Very lightly exploited	Allocation requirements may reduce rates of exploitation.
Pacific sardine	California, N. Baja California	428	91	10	3	some (bait)	0	large	[2]300-500	Depleted	Rehabilitation unlikely in near future.
Pacific mackerel	Central California to central Baja California	30	20	16	1	33	33	34	[3]30-50	Depleted	Rehabilitation unlikely in near future
Jack mackerel	West coast of North America	34	38	39	24	0.1	89	11	210-450	Probably lightly exploited	Size of local stock is indeterminate, but large.
California barracuda	Southern California to central Baja California	2.1	1.9	1.2	0.5	48	2	48	[4]1-2	Depleted	Rehabilitation possible in near future.
Yellowtail	Southern California and Baja California	3.1	3.2	1.2	1.5	67	13	20	[4]3-6	Lightly exploited	Migration into Calif. is heavily exploited.
Pacific bonito	California and Baja California	2.7	1.4	7.6	11.8	11	87	2	10-20	Probably moderately to highly exploited	Biomass and potential highly fluctuating with recruitment. California residency may be a temporary event.
White sea bass	California and Baja California	0.5	1.0	0.6	0.5	8	76	17	0.8	Moderately/highly exploited	Indices of abundance conflict

[1] At the 1970-1973 population level.

[2] If rehabilitated to the pre-1944 population level.

[3] If rehabilitated to the pre-1950 population level.

[4] The California yield is influenced by ocean temperature.

population may be overestimated by commercial fishery data and underestimated by partyboat data—a phenomenon that currently is being examined. We have investigated some of the potential results of various future developments in the sport and commercial fisheries which may be of use in management decision-making.

The status of the **California barracuda** stock is difficult to assess with respect to a definite level of MSY, but appears to be at a low level. Length frequency indicates a preponderance of very young fish in recent partyboat catches and it is possible that the previous allowance of fish shorter than 28 inches in bag limits has contributed to depleted spawning stock and consequently reduced recruitment. Maintenance of the present strict observance of 28-inch minimum length is a rational course of action. There appears to be sufficient stock remaining to engender optimism regarding rehabilitation of the resource in the next decade, given favorable environmental conditions. Abundance of barracuda off California is strongly influenced by ocean temperatures.

Pacific bonito appears to be a relative newcomer to the sport catch, having been absent for a number of years prior to 1956, and large-scale commercial fishing has increased to unprecedented levels in the past few years. Sport availability is an indicator of recruitment and is highly correlated with abundance of commercially exploitable fish 3 years hence. A crude production model indicates that bonito are presently being harvested at or above MSY (although the assessment is confounded by the possibility of a density-independent decline in recruitment). The 1973 catch appears to be considerably in excess of equilibrium yield. However, since Pacific bonito fishing success is influenced by ocean temperatures, conclusions drawn from the crude production model must be accepted with caution.

While it would be desirable to assess the stocks of other species, such as Pacific hake, saury, squid, and the rockfish group, the limited amount of data available for the southern California Bight prevents such undertakings. **Rockfish** appear to be abundant in southern California waters and are becoming progressively more important as a sport fishing resource. Separation of rockfish partyboat effort should lead to feasibility of southern California stock assessment for that species complex. **Squid** is receiving increased attention from commercial fishermen and marketers and is an important candidate for stock assessment. If a series of annual squid abundance estimates becomes available (such as by aerial survey), assessment by methods similar to those used for bonito should be possible.

Studies of interactions were brief, due to the extreme complexity of the subject. The northern anchovy fishery has a large number of interacting elements, and regulation is poorly coordinated. The southern California live bait fishery is a very important user of anchovies, and has occasionally reported poor bait availability, allegedly due to commercial fishing. Our results indicate that the availability of anchovies to the live bait fleet has increased considerably over the long term, and that while there may be a slight reduction in relative availability in the winter reduction season, the difference is very small and even of questionable existence. The Santa Barbara bait fleet appears to be anomalous in many respects, and may be in real difficulty, although it is difficult to attribute its problems to the anchovy reduction fishery.

Multiple species aspects of fisheries received brief attention. Quality of sport fishing seems to have been very good during the late 1950's and most of the 1960's. Sport fish now appear to be returning to levels typical of the early

1950's with respect to abundance of large and medium sport fish, although species composition is now different. This seems to be associated with the warm water period beginning in late 1956 and continuing into 1960. The commercial wetfish fleet appears to be flexible in its choice of target species and has gained independence of the availability of sardines.

An analysis of trophic interaction indicates that while both forage (anchovies and sardines) and game fish (yellowtail, bonito, albacore, barracuda, and white seabass) increased in abundance between the 1950's and 1960's, there seems to be little evidence that either prey or predator biomass shows strong dependence on the abundance of the other. It appears more likely that the abundance of both is determined largely by external conditions. If any interdependence is in effect, it should have been much weaker in the 1960's than in the late 1950's.

DATA AND METHODS

The following report briefly documents the analytical methods and data used for the "quick" stock assessment of some of the more important recreational and commercial fisheries of southern California. The analyses of the various stocks utilized similar methods and types of data, making a general discussion of procedures appropriate.

Stock assessment methods

Stock assessment methods were applied in a manner to give the most rapid assessment of fisheries stocks. Sophistication and accuracy are desirable, but suffer low priority in the face of an urgent need for information on critical fishery problems. Often the quick solution will serve as a guide in long-term investigation of problems, and can be considered as a "first cut."

Stock assessment procedures have three time-consuming operations: 1) collection of data, 2) development and refinement of models, and 3) justification and elimination of assumptions. Expedient methods minimize these steps. Only available data are used; where data are missing, reasonable estimates are made in order to fill the gaps. Methods tend to be restricted to application of very simple models. These are further simplified by relaxation of statistical procedures and tests of validity in favor of approximate solutions. Whereas in the more detailed investigations, considerable work is devoted to attempts at eliminating or justifying assumptions, "quick and dirty" methods rely on assumptions as a modus operandi. Within the constraints of generating a useful and meaningful report and of conforming to knowledge and information regarding the subject, all reasonable assumptions necessary to pursuance of the investigation are justified. The extent to which fundamental assumptions, which significantly influence conclusions, are not met in the real world, will affect the accuracy of the conclusions.

This investigation attempts to determine the status of fish stocks and their level of exploitation. Status, however, is a vague term, and may have different criteria for different users, particularly in the case of sport fishermen and commercial fishermen. We have used MSY as a standard criterion in these assessments for several reasons: MSY is a measurable quantity, and is the standard parameter determined from application of simple fisheries yield models; moreover, MSY is a likely upper bound for optimum sustainable yield whether the optimizing criterion be economic value, stability of yield, or recreational value. Optimum sustainable yield criteria are the subject of further investigation. Thus, we do not wish to imply, in assessing status relative to MSY, that catches should necessarily be brought to such levels. However, if MSY is exceeded, a reduction in fishing effort is to be strongly recommended.

Data

The most important information to fisheries assessment and management is total catch. The first step (besides familiarization with the species and fisheries) in these investigations was to compile a complete table of catches since about 1950. This required collation of data furnished by many sources (Table 2), both published and otherwise. Where data were unavailable, estimates were based on available information, suspected trends, and educated opinions. In many cases, the time series of catches for a particular fishery segment were estimated by the ratio of catch available for years indicated in Table 2 to known catch of a similar fishery.

In order to make all catches comparable, and for use in surplus production models, catches were converted to estimates of weight. This task presented no obstacle in the case of the commercial fisheries, where landings are already recorded in weight, and in the bait fishery, where the weight to volume ratio is approximately constant (15 pounds/scoop). In the sport fisheries, however, the problem is not as simple. Average weights per fish were calculated from length frequencies via weight-length formulae. For most sport species, length frequencies were available only for a few years in the 1950's from special studies of the California Department of Fish and Game (CDFG). Fortunately length-frequency

Table 2.—Catch data sources.

Catch	Source	Years	Availability	Units
Commercial				
California				
California waters	CDFG	1916-present	Published (CDFG Fish Bulletins)	Weight
Mexican waters	CDFG	1916-present	Published (CDFG Fish Bulletins)	Weight
Bait	Voluntary (CDFG)	1951-present		Volume
Mexico	INP	1962-present	Published (FAO Yearbook of Fishery Statistics)[3]	Weight
	FAO	1961-present		Weight
Sport				
California				
Local partyboat	CDFG	1936-40	Published (CDFG Fish Bull. 86)	Number
		1947-present	Published (Young, 1969)	Number
Long range partyboat	CDFG	1960-present		Number
Barge	CDFG	1947-present		Number
Private boat[1]	CDFG	1964	Published (Pinkas et al 1968)	Number
Pier and jetty[1]	CDFG	1963	Published (Pinkas et al, 1967)	Number
Shoreline	CDFG	1965-66	Published (Pinkas et al, 1968)	Number
Mexico				
Partyboat	Voluntary (ESFA)[2]	1961, 1971		Number

[1] Program in progress 1973, 1974

[2] ESFA-Ensenada Sport Fishing Association, supplied through Instituto National de Pesca (INP)

[3] Tend to lack sufficient specificity for stock assessment.

sampling of sport catches has been recently instituted by CDFG. The 1972 and 1973 length frequencies made available by it were a great benefit to the stock assessments. Where length frequency was lacking, reasonable estimates were again employed.

The second important parameter necessary for stock assessment is an index of stock abundance. Traditionally this is obtained by measuring effort and calculating catch-per-unit-effort (CPUE) which is presumably proportional to stock abundance[1]. Effort was available for commercial white seabass and for the southern California partyboat sport fishery in general, wherein no distinction was made between species sought.

Partyboat effort and CPUE were adjusted to account for the change in the unit of effort from "angler-days" to "anglers" (angler-trips) and for regional differences between sizes of fishing area (Table 3). Conversion ratios for adjusting effort for the period 1947 to 1960 were estimated from 1960 and 1961 data in which both units were recorded. The variation of conversion ratios within regions was much smaller than between regions. The ratios were significantly different between regions based on an analysis of variance with years as replicates ($F = 56.7, d.f. = 5, 6; P\ (F>4.39) = 0.05$). As a result effort was adjusted for each region separately.

Abundance indices were calculated from partyboat catch-effort data in three ways. First, annual catch divided by annual effort for all areas combined was called CPUE. This was used when comparisons with early years were desired, as only total California catch was available for 1936-40. Second, annual catch per annual effort for the San Diego region alone was used as a possible index of abundance, San Diego being presumably closest to the population centers of our migratory southern species. Third, a "CPUE index" was calculated as the weighted average of annual CPUE's of the six regions. Weights were determined by estimating the area of water less than 20 fathoms deep in the geographical area in which each region's effort was presumably exerted (Table 3). In view of lack of statistical information on geographical distribution of effort, arbitrary non-overlapping areas were used. Effort according to CDFG block origins was consistent with effort reported from each landings region. The "CPUE index" was felt to be the best partyboat CPUE-based index of abundance in most cases, but no other comparable abundance indices were available to verify this.

Table 3.—Effort unit conversion and area weighting factor.

Region	Conversion[1]	Area weighting factor[2]
San Diego, Mission Bay	1.201	0.19
Dana Harbor, Oceanside	1.318	0.10
Huntington Beach, Balboa	1.121	0.05
San Pedro, Long Beach	1.271	0.12
Malibu, Redondo Beach, Santa Monica	1.591	0.11
Santa Barbara, Port Hueneme	1.010	0.43
Total, Southern California	1.215	1.00

[1] Anglers/angler day

[2] Depth ≤ 20 fathoms.

Other abundance indices used in these investigations included aerial, acoustic, and egg-and-larva surveys, which are best for pelagic schooling fish. Squire's (1972) day and night aerial indices of abundance were recalculated to include only the southern California area (regions A and B were excluded). Acoustic surveys carried out by CDFG were useful in measuring anchovy abundance, but due to lack of sufficient overlap with egg-and-larva abundance surveys verification of acoustic estimates by correlation methods is unfeasible. Egg-and-larva surveys were also useful for jack mackerel and sardines. Recent CDFG tagging of jack and Pacific mackerel provided useful biomass estimates for those species.

Separation of stocks was given little emphasis as such problems could not be resolved with available data. Where geographical limits for stocks were lacking, all catches were assumed to have come from a single panmictic stock.

Population parameters such as those for growth, length-weight, and mortality were generally available from published sources or were in press. Where values were lacking, reasonable estimates were used, or, in the case of white seabass natural mortality, a new estimate (described in more detail later) was made from more recent data. Individual estimates and assumptions are generally noted in the sections in which they occur, but many escape discussion.

Methods

Wherever possible, stock status was determined by a surplus production or "Schaefer" model, which in practice consists of plotting abundance as catch per effort against a mean effort averaged over half the fishable lifetime of the fish (Gulland, 1970). Usually effort (fishing mortality) is assumed to be related to the amount of fishing done by the exploiting fleets. A total effort index may be derived from catches and abundance indices that are somewhat independent of the fishing fleets, such as the aerial index, as was done for Pacific bonito. The presumably steady-state relationship between effort and abundance will generally show as decreasing CPUE with increased effort. A line describing this relationship is sketched in, or a straight line (sometimes not best approximation) can be statistically fitted to the observations. An approximation of an equilibrium yield curve can then be calculated by multiplying together the coordinates of the equilibrium abundance line (catch per effort × g effort = catch), and plotting against the same effort axis as in the previous plot. This will usually give a concave downward paraboloid curve (a true parabola results from the straight-line fit mentioned previously), and estimated MSY corresponds to the peak of the yield curve. Extrapolation of the equilibrium yield curve beyond points of observation (particularly toward greater effort) should be interpreted with caution, as MSY's and corresponding effort levels obtained in this manner are very imprecise. For most of the stocks investigated in this study, MSY fell within the observed spread of values.

This approach assumes that CPUE, particularly sport CPUE, is proportional to stock biomass. Changes in gear efficiency (e.g., introduction of monofilament line in the mid 1950's) may increase catchability, and artificially increase CPUE. More important, CPUE is influenced by the availability of fish. The northern migration of game fish such as yellowtail and barracuda from their population centers off Baja California into southern California waters is greatly influenced by oceanographic conditions. The apparent abundance, measured by sport CPUE, depends in part on the extent of this northern migration. The large catches during the warm water years of the late 1950's are examples. For the purpose of this report, the data points for these years are treated as outliers in the surplus production models.

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[1] Recent studies suggest that CPUE may not be linearly proportional to population size.

For relatively unfished stocks, where biomass is many times larger than catch, as in the case of jack mackerel and northern anchovy, the surplus production model cannot be applied. In this case, we have used Gulland's (1970) approximation of MSY based on unfished biomass and natural mortality, which is itself postulated on surplus production concepts.

The Gulland formula is $Y_{pot} = XMB_0$ where Y_{pot} is potential yield, M is instantaneous natural mortality rate, and B_0 is mean virgin biomass of fish above length at first capture. X is a coefficient which is determined by M, K (von Bertalanffy growth rate)[2], and length at first capture relative to maximum length. Values for X tend to fall around 0.5, which is a reasonable value if other parameters are unknown. Yield values obtained by this method are recognized as first approximations, to be revised by more precise methods as a time series of catch and effort (or abundance) is acquired.

In fisheries where spawner-recruit relationships are obscure and surplus production models give inconclusive results, we have attempted to investigate yield per recruit (Y/R) as a basis for evaluating minimum length restrictions. We found the short-cut yield tables in Beverton and Holt (1966) very useful for this purpose. Where multiple fisheries interaction raised a particular problem, as in the white seabass, a complex Y/R analysis (Lenarz, Fox, Sakagawa, and Rothschild, 1974) was employed.

NORTHERN ANCHOVY

This report of northern anchovy, *Engraulis mordax*, is an overview of the relationship between present harvest levels and potential yields of the stock. Further investigations of the complex interactions between resource uses, live bait, reduction, and sport fish forage are not considered for best allocation of resource. These are briefly discussed elsewhere in this document.

Table 4.—Northern anchovy, biomass estimates and indices of abundance.

Year	Overall population		Central stock (Southern California and northern Baja California)				
	Egg and larval surveys			Acoustic survey	Aerial surveys		Spawning biomass extrapolated from regression between (3) and (5) (10^3t) (7)
	Ratio anchovy spawning biomass[1] (10^3t) (1)	Regression anchovy spawning biomass[1] (10^3t) (2)	Spawning biomass[1] (10^3t) (3)	Annual mean of surveys[2] (10^3 schools) (4)	Night index[3] (5)	Day index[3] (6)	
1940	2.359						
1950	279						
1951	690	637	294				
1952	856	797	410				
1953	(1.404)	1.335	807				
1954	1 937	1.816	855				
1955	1.855	1.676	1.386				
1956	1.307	1.491	919				
1957	1.869	1.964	1.576				
1958	2.875	2.771	1.832				
1959	(2.418)	2.299	1.686				
1960		3.079	1.918				
1961		3 189	1 264				
1962		6.248	4.362		1.57	0.045	
1963		6.030	4.861		2.24	0.50	
1964		5.121	3.866		3.86	0.57	
1965		7 771	6.211		4 08	0.71	
1966		5.116	4.154	107	3.05	0.86	
1967				174	5.14	2.02	4.784
1968		(2.167)	(2.048)	195	1.35	0.30	
1969		3.378	2.993	103	4.39	1 34	
1970				56	[4](7.46)	[4](6.65)	
1971				101	3.23	1.26	4.166
1972				194	1.41	1.33	3.577
1973				275			
1974				(362)			

[1] After P Smith 1972, tables 9 and 12 and figure 13, and A Vrooman and P Smith 1971 table 2 Column (1) is derived from a ratio of anchovy larvae to sardine larvae relative to estimated sardine spawning biomass; column (2) is derived from the regression of this estimated anchovy spawning biomass on anchovy larvae

[2] Information provided by K. F. Mais CDFG

[3] After J Squire, 1972, table 7, completed with recent yet unpublished data.

[4] Six months only

Biomass

Estimates or indices of abundance for the northern anchovy have been obtained through various independent methods, i.e., egg-and-larva, acoustic, and aerial surveys (Table 4). Separate data are available by geographical areas, months, or quarters. According to estimates from eggs and larvae collected during 16 years, the subpopulation centered off southern California and northern Baja California (the central stock) makes up 66 percent of the overall total spawning biomass (range of annual values: 40-83 percent) but in years since 1963 the ratio has been about 80 percent. Acoustic surveys from 4 years confirm the above estimate (range 65-86 percent). Increase in the central stock accounts for the increase in total biomass of the northern anchovy since 1950 (Fig. 1). Because of this and its proximity to the California fishing fleet, only the central stock is considered here.

Estimates derived from egg-and-larva surveys, which may be our most reliable source, correspond only to the spawning biomass while data from other sources may include biomass of immature fish. Therefore, the estimates are not directly comparable. Insufficient information regarding age at first maturity does not permit precise assessment of the ratio of total biomass to spawning biomass. However, as the majority of fish appear to be mature at 1 year (Knaggs, CDFG[3]), which also corresponds to approximate age of recruitment to the fishery, exploited biomass should not be substantially higher than spawning biomass. As a first approximation, spawning biomass is used here as exploitable biomass. If it would be possible to expand exploitation upon juvenile stages, the exploitable biomass would exceed spawning biomass.

Various estimates and indices have been compared. Correlation coefficients between the independent methods for years in which the surveys have coincided are given in Table 5. Correlations are in general not high and positive only in the case between estimates derived from egg-and-larva surveys and night aerial surveys. The apparent contradiction between acoustic surveys and night aerial surveys may result from the fact that these two methods do not actually sample the same portion of the overall biomass. Acoustic surveys may not suitably detect fish occurring close to the surface, while aerial surveys record only fish concentrations visible in the upper layer of the sea. An important source of error is the fact that sonar-based acoustic surveys have been employed only since 1969. Data for 1966 and 1967 have been inferred from echo-sounding surveys. The biomass estimates from the egg-and-larva surveys and indices from the aerial surveys are in more agreement particularly when night sightings are considered. As observed by Squire (1972), this may be due in part to higher efficiency of aerial surveys conducted at night as compared with daytime observations. A correlation coefficient cannot be calculated for egg-and-larva survey estimates and acoustic data because the time series do not overlap enough. On the other hand, acoustic estimates of biomass tend to agree with egg-and-larva estimates when schools are assigned an arbitrary—but likely—average value of 17 tons (Smith, 1970), or when expanded to volume and assigned a packing density of 50 fish/m^3 (Mais, pers. commun.). Considering general knowledge on reliability of egg-and-larva survey methodology, together with the extent of sampling done both in time and space, it is assumed that biomass estimates used here provide a picture of the stock sufficiently accurate for present assessment problems.

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[2] The von Bertalanffy growth curve is $l_t = L_\infty (1 - e^{-k(t-t_0)})$ where l_t is length at time t, L_∞ is asymptotic maximum length, k is a growth rate constant, and t_0 is hypothetical age at zero length.

[3] E. Knaggs, CDFG, 350 Golden Shores, Long Beach, CA 90802. Pers. commun.

Table 5.—Comparison of biomass estimates and indices of availability obtained through various methods.

Source	Correlation coefficient	Years of observation
Acoustic surveys/ aerial surveys (night)	−0.47	1966, 67, 68, 69, 71, and 72
Acoustic surveys/ aerial surveys (day)	−0.08	1966, 67, 68, 69, 71, and 72
Egg-and-larva surveys/ aerial surveys (night)	+0.30	1962, 63, 64, 65, 66, 68, and 69
Egg-and-larva surveys/ aerial surveys (day)	−0.05	1962, 63, 64 65, 66, 68, and 69

Table 6.—Northern anchovy catches in short tons.

Year	U.S. commercial	U.S. bait	Mexico commercial	Total
1973	110,885	(6,000)	10,613	(127,498)
1972	69,101	(6,000)	[1](60,000)	(135,101)
1971	44,853	6,387	(40,000)	(91,240)
1970	96,243	6,105	(55,000)	(157,348)
1969	67,639	5,314	4,258	77,211
1968	15,538	7,177	15,694	38,409
1967	34,805	5,387	22,115	62,307
1966	31,140	6,691	14,567	52,398
1965	2,867	6,148	10,088	19,103
1964	2,488	5,191	5,059	12,738
1963	2,285	4,442	1,039	7 766
1962	1,382	6,167	736	8,285
1961	3,856	5,913	(500)	(10,269)
1960	2,529	4,658	(500)	(7,687)

[1] Estimated from informal sources.

Table 7.—Central stock: biomass (*B*), annual catch (C), and fishing mortality (*F*) during the 1968-73 period.

Year	Central stock spawning biomass (10^3 tons)	Estimated annual catches (10^3 tons)	$F = \frac{C}{B}$
1968	2,048	59	0.03
1969	2,993	114	0.04
1970	—	157	—
1971	(4,166)	91	0.02
1972	(3,577)	135	0.04
1973	—	132	—

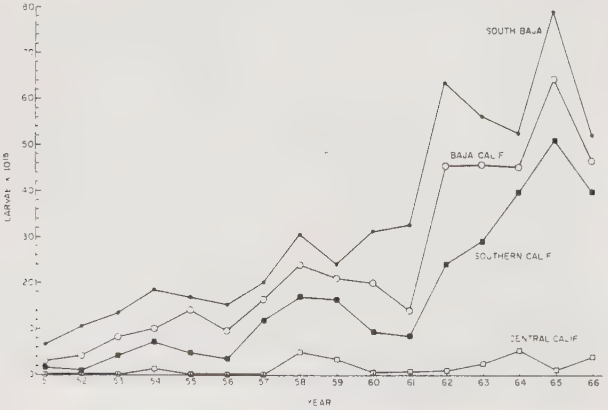

Figure 1.—Time series comparison of the annual total census estimates of anchovy larvae as grouped by coastal section (from Smith, 1972).

Indices derived from nighttime aerial surveys were regressed on concurrent estimates of the spawning biomass of the central stock to estimate the biomass in 1967, 1971, and 1972 (column 7, Table 4) for which no egg-and-larva surveys are available.

Catches

Catch statistics for the 1960-73 period are given in Table 6. These data refer to the central stock which is essentially the only one exploited. The mean lengths of the catches for successive years have decreased. The trend and year-to-year fluctuations can be caused by changes in recruitment and natural mortality rates, exploitation, and/or size selection of the fishery. (Average lengths of fish in catch[4]: 123.0 mm in 1965-66; 123.1 mm, 1966-67; 120.5 mm, 1968-69; 120.9 mm, 1969-70; 127.5 mm, 1970-71; 116.1 mm, 1971-72; and 116.0 mm, 1972-73.)

Maximum potential yield

Fishing mortality (*F*) can be derived from catch data and biomass estimates (Table 7). The *F* values confirm that the rate of exploitation has been very low. Considering that, as mentioned above, biomass estimates do not include the juvenile stages, fishing mortality may be lower than the average value of 0.03 observed from 1968 to 1972.

Total mortality has been calculated by MacCall (1973) from catch curves for 5 different years. The value of $Z = 1.1$ thus obtained indicates that natural mortality M cannot be smaller than 1.00-1.05. Spratt (1975) gives values of 0.3 and 165.5 mm (standard length) for von Bertalanffy growth curve parameters K and L_∞, respectively. The average size at first capture, l_c, is not exactly known, since recruitment occurs during a rather long period (affecting individuals from about 85 mm to 115 mm). In the following calculations, the value of 105 mm has been used.

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[4] From Messersmith (1969), Collins (1971), Spratt (1972, 1973a, b), and Sunada (1975).

Considering that the stock is very near to virgin state, Gulland's equation $Y_{pot} = XMB_0$ can be used for assessing the maximum potential yield. With $M/K = \frac{1.05}{0.3} = 3.5$ and $c = \frac{l_c}{L_\infty} = \frac{105.0}{165.5} = 0.63$, the coefficient X would be about 0.6 (Gulland. 1970, p. 3). The maximum potential yield should therefore be about 60 percent of the fishable biomass. As the latter has shown considerable fluctuations during the years under observation, several values of potential harvest can be derived (Table 8).

From the analysis of available data, it can be concluded that the central stock of northern anchovy can produce a yield from 10 to 20 times higher than present catches. There is some information that Mexico is considering development of its present production to about 500,000 tons, of which 200,000 tons would be caught by vessels operating from Ensenada. If this occurs, such vessels will most likely exploit the central stock. This target catch represents about one-eighth of the potential of the central stock as derived from biomass estimates for the period 1951-72 and about one-thirteenth of its potential when calculated for years following the collapse of the Pacific sardine stock. The USSR has also shown interest in offshore trawling for anchovies, with possible catch rates as high as 25,000 tons per ship-year. Their ultimate catches are likely to depend on success of the venture and the course of international law.

Size of first capture

On the basis of available values of M, K, l_c, and L_∞, yield per recruit tables indicate that a reduction of size at first capture would lead to considerable gain, if the fishery were unrestricted and if juveniles were fully vulnerable to fishing gear. For example, with the present rate of exploitation ($E = 0.05$), if the size at first capture were at 90 mm instead of the present assumed value of 105 mm, both annual yield and catch rates would, in theory at least, double. Because of the high rate of natural mortality of anchovy, even for high rates of exploitation (e.g., $F/Z \simeq 0.8$) maximum yields and catch rates would be achieved with sizes at first capture below 80 mm. Therefore at the present level of exploitation, it does not seem reasonable from Y/R to implement in California regulatory measures aimed at limiting the size at first capture or the allowed landing sizes.

Conclusions

At present the potential yield of northern anchovy can be estimated at above 2 million tons. Remembering that biomass estimates used in this appraisal include only the spawning population, this resource may even be substantially larger than in the figures given in Table 8. Because of high natural mortality of anchovy, there is no need to limit the size at first capture in California at the present level of harvest. In this context, it should be stressed that the stock apparently shows very large year-to-year fluctuations. Therefore, in the event that substantially higher levels of exploitation are considered, careful monitoring of the stock abundance and size composition would be essential in order to prevent overexploitation during periods of successive low recruitment.

BARRACUDA

The California barracuda, *Sphyraena argentea*, fishery has undergone a long decline, beginning in the 1930's and ending with the present virtual extinction of a commercial fishery and the maintenance of a stable but unacceptable sport fishery in which only small fish are available. Here we attempt to assess the present status of the stock.

Data

Catch records for barracuda are similar to those of other recreational species. Long time series of catch records in weight are available for U.S. commercial fisheries operating in California waters and off Mexico, and records in number for California partyboat catch and Mexican commercial catches are known since 1966. Catches for other fishery segments were estimated from data for specific years as footnoted in Table 9. Sport fish catches were converted to weights by using available length frequency data and the length-weight curve given by Walford (1932), and from weight given by Baxter and Young (1953). Length frequency data for the California partyboat fishery are available for the years 1958, 1959, 1960, and 1961 (Pinkas, 1966) and 1972 and 1973 (D. L. Schultze, CDFG pers. commun.). The 1972 and 1973 samples are not representative of the landings because undersized fish that were released after capture were included. A constant 4.9 pounds/fish was assumed for the 1936-51 period (Baxter and Young, 1953). No weight samples are available for the period from 1952 to 1957. Mean weight values for the sport-caught fish were not assumed for this period because the fishery declined during these years but immediately increased with the start of the warm water years. Mean weights of 4.16, 3.87, 2.64, and 2.59 pounds/fish for 1958, 1959, 1960, and 1961 respectively were estimated from mean lengths given in Pinkas (1966). An estimate of 2.6 pounds/fish based on the 1961 samples was applied to all following years through 1970. Because the two undersize fish (less than 28 inches) allowance in the bag limit was eliminated, a value

Table 8.—Biomass and corresponding potential yields for the total population and the central stock for 1) the 20-year period of observation and 2) after the depletion of Pacific sardine stock.

Time period	Population	Biomass mean and range (10^3 tons)	Corresponding potential yields (10^3 tons)
1951-69	Total	3,200 (640-7,800)	1,900 (400-4,700)
1951-72 after sardine collapse	Central stock	2,600 (290-6 200)	1,500 (200-3,700)
1965-69	Total	4,600 (2,200-7,800)	2,800 (1,300-4,700)
1965-72	Central stock	4,000 (2,050-6 200)	2,400 (1,200-3,700)

Table 9.—Catches of California barracuda for various fisheries.

	U.S. commercial			Sport						
Years	California (lb)	Mexico (lb)	Mexico commercial (lb)	Partyboat California (fish)	Other California (fish)[1]	Mexican waters (fish)[2]	Total (fish)	Total est. weight (lb)	Total commercial and sport (lb)	Fraction sport
					< 1,000					
1928	4385.2	2067 2								
1929.	3925.9	1302.7								
1930	3513.6	1250.2								
1931	3336.1	841 5								
1932	2505.1	421 7								
1933	2912.2	160.8								
1934	1801.3	381.6								
1935	2003.9	613.9								
1936	2247.9	730.0		492.5			(500)	(2450)	(5428)	0.45
1937	1799.0	1139.4		598.5			(600)	(2940)	(5878)	0.50
1938	1260.8	1269.0		314.2			(320)	(1568)	(4098)	0.38
1939	2969.2	1122.8		663.5			(670)	(3283)	(7375)	0.44
1940	2545.4	1151.9		704.5			(710)	(3479)	(7176)	0.48
1941	2971.3	1230.6							(4202)	
1942	2243.2	1211.4							(3455)	
1943	2382.8	1392.5							(3775)	
1944	2317.3	1330.9							(3648)	
1945	1744.6	2110.7							(3855)	
1946	1636.1	1470.4							(3107)	
1947	1695.9	969.9		677.4	(10)	(10)	(697)	(3415)	(6081)	0.56
1948	1100.1	1025.7		384.1	(20)	(20)	(424)	(2078)	(4204)	0.49
1949	903.6	1570.3		366.4	(30)	(30)	(426)	(2087)	(4561)	0.46
1950	890.4	1368.0	(0)	256.4	(33.7)	(41 0)	(331.1)	(1622.4)	(3880.8)	0.42
1951	670.0	1436.9	(10)	269.5	(35.4)	(51.2)	(356.1)	(1744 9)	(3851 8)	0.45
1952	747.7	1346.5	(20)	336.9	(44.3)	(74.1)	(455.3)	(1365 9)		
1953	565.9	872.9	(30)	170.6	(22.4)	(37.5)	(230.5)	(691.5)		
1954	485.9	1076.8	(40)	282.6	(37.1)	(79.1)	(398.8)	(1196 4)		
1955	322.8	818.1	(50)	155.0	(20.4)	(48.0)	(223.4)	(670.2)		
1956	50.2	702.4	(60)	87.6	(11 5)	(29.8)	(128.9)	(386.7)		
1957	387.1	295.5	(60)	577.2	(75 9)	(213.6)	(866.7)	(2600.1)		
1958	753.3	162.0	(60)	782.8	(102.9)	(313.1)	(1198.8)	(4987.0)	(5962.3)	0.84
1959	1110.4	42.2	(60)	1195.6	(157 2)	(478.2)	(1831.0)	(7086.0)	(8298.6)	0.85
1960	1147.8	81.8	(60)	755.4	(99.3)	(302.2)	(1156.9)	(3064 2)	(4353.8)	0.70
1961	478.4	231.0	(60)	391.9	(51.5)	111.4	(554.8)	(1446.3)	(2215.7)	0.65
1962	521 8	224.7	79.5	335.5	(44.1)	(134.7)	(514.3)	(1337 2)	(2163.2)	0.62
1963	347.4	31.4	41.4	483.7	(63.6)	(193.8)	(741.1)	(1926 9)	(2347.1)	0.81
1964	251.0	83.1	99.8	303.1	(39.8)	(122.8)	(465.7)	(1210.8)	(1644.7)	0.75
1965	273.0	89.1	60.3	443.3	(58.3)	(178.3)	(679 9)	(1767.7)	(2190.1)	0.81
1966	233.3	85.8	61.9	892.7	(117.3)	(358.4)	(1368.4)	(3557.8)	(3938.8)	0.90
1967	281.2	32.0	32.8	470.5	(61 8)	(190.4)	(722.7)	(1879.0)	(2225.0)	0 84
1968	114.5	26.0	14.4	372.2	(48.9)	(150 4)	(571 5)	(1485.9)	(1640.8)	0.91
1969	70.8	3.8	9.2	358.5	(47.1)	(149.3)	(554.9)	(1442.7)	(1526.5)	0.95
1970	22.5	2.1	3.3	373.8	(49.1)	(154.2)	(577.1)	(1500.5)	(1528.4)	0.98
1971	17.3	0.0	6.6	50.5	(6.6)	194.7	(251 8)	(638.6)	(662.5)	0.96
1972	13.9	0.0	(5)	38.2	(5.0)	(154.0)	(197.2)	(591.6)	(610.5)	0.97
1973	37.6	0.0	(15)	92.5	(12.2)	(370.9)	(475.6)	(1426.8)	(1479.4)	0.96

[1] Other California sport landings estimated as 0.1315 California partyboat landings

[2] Mexican sport landings estimated as long-range partyboat catch plus 0.4 (declining to 0.16 from 1958 to 1950) of California partyboat landings

of 3.0 pounds/fish was used for 1971, 1972, and 1973. Length frequency data are also available for the California commercial fisheries for the years 1928 (Walford, 1932), 1958, 1959, 1960 (Pinkas, 1966), and 1973 (D. L. Schultze, CDFG, pers. commun.)

California partyboat records on catch and angler effort provide the only index of abundance. The aerial survey (Squire, 1972) recorded too few sightings of barracuda to be useful. Egg-and-larva surveys gather barracuda larvae but the data as of yet have not been processed. It is not known if the observations are sufficient to provide an index of abundance.

Historical trends

Total landings of barracuda have generally declined since the mid-1930's except for short term peaks in 1966 and in the warm water years of 1957-60 (Figure 2). The U.S. commercial fishery landed an annual average of 3,800 short tons of barracuda during 1920-25. These decreased to 1,400 tons annually for the years 1932 through 1938, and then increased to 1,900 tons for 1939-45. After 1945 the commercial catches steadily declined to the present level of 5-20 tons. However, from the beginning of sport fishing records in 1936, sportsmen consistently landed approximately 1,200 tons annually prior to 1952. During the warm water years, when barracuda were considerably more available, annual sport catches ranged from 1,300 to 3,500 tons. Prior to 1951 the sport catch amounted to 46 percent of the total landings but since 1968 it has made up more than 90 percent of the total.

Examination of the length frequency samples from U.S. commercial and from partyboat fisheries suggests that the barracuda stock presently lacks the larger size groups (Figs. 3, 4). The length frequencies for the commercial fishery may differ somewhat due to changes in fishing gear. The method of capture was predominantly purse seines in 1928, gill nets and jigs from 1958 to 1960, and gill nets in 1973. Since samples for years 1952 to 1957 do not exist, it is not known if the above trend started in the early 1950's or early 1960's. The warm water years are associated with an extensive northward migration of the barracuda population. Occurrence of large fish in these samples may be a result of this migration. The decline in frequency of larger fish may have paralleled the decline in catch rather than the abrupt change suggested by the length frequencies available. In any event, the

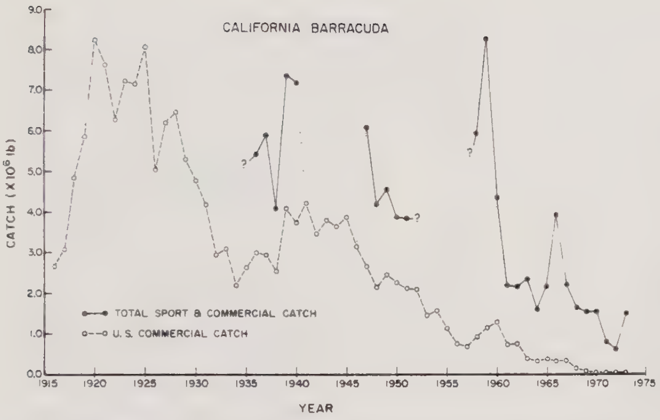

Figure 2.—California barracuda U.S. commercial landings (1916-1973) and estimated total landings (1936-1973).

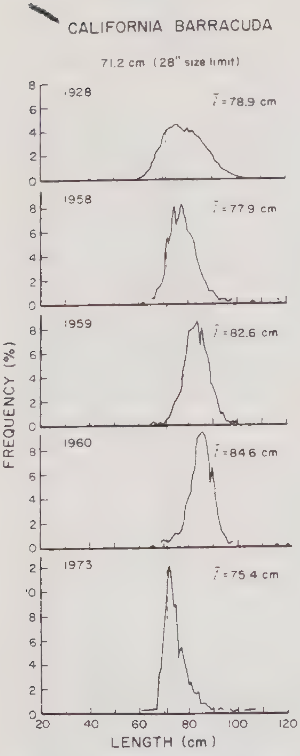

Figure 3.—Length frequencies for California barracuda from U.S. commercial fishery for 1928 (Walford, 1932), 1958, 1959, and 1960 (Pinkas, 1966) and 1973 (D. L. Schultze, CDFG, pers. commun.)

fishery has harvested the younger age groups, particularly 2-, 3-, and 4-year old fish in recent years.

The number of sport-caught undersize barracuda permitted per bag has been altered a number of times. Between 1933 and 1949 sport fishermen were allowed not more than five fish weighing less than 3 pounds each. Between 1949 and 1957 the undersize allowance was five fish less than 28 inches. These size limits were effectively identical since a 28-inch barracuda weighs approximately 3 pounds (age 5 years). The allowance was reduced to two undersized fish per bag in 1957. In March 1971 the possession of barracuda under 28 inches was prohibited altogether. As it is illegal to possess undersize barracuda, sport fishermen release a large number of undersize fish as indicated in length frequency samples for 1972 and 1973 (Fig. 4). If the released fish have poor survival, the beneficial effect on the stock may be reduced and/or retarded.

The CPUE (Σ catch in weight/ Σ anglers) for the U.S. partyboats has two periods of extreme highs, the years prior to 1948 and the warm water years (Fig. 5). If these extremes are eliminated, the two remaining sequences are somewhat level. On the other hand each segment shows a decline in itself.

The CPUE index in numbers of fish for all regions combined was compared to the CPUE for the San Diego region only (Fig. 6). For many of the years, the points lie well above the 1:1 line, which means that the sport catch rate was high in the San Diego region, yet relatively low overall. This suggests that the barracuda migrations in the early 1950's

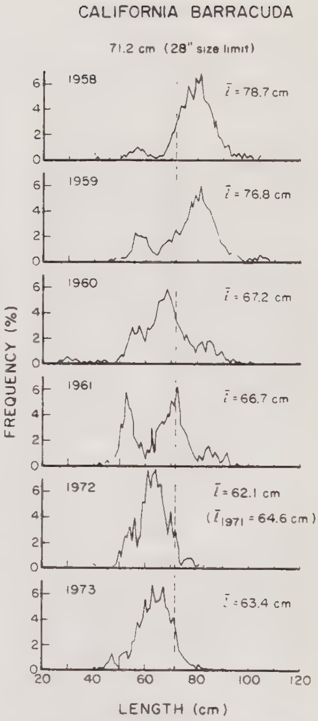

Figure 4.—Length frequencies for California barracuda from U.S. commercial partyboats for 1958, 1959, 1960, 1961 (from Pinkas, 1966) and 1972 and 1973 (D. L. Schultze, CDFG, pers. commun.)

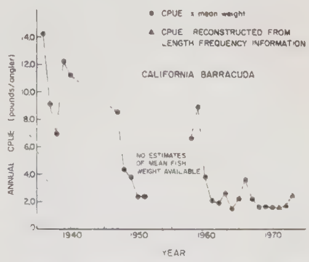

Figure 5.—California barracuda partyboat CPUE for years 1936-1970.

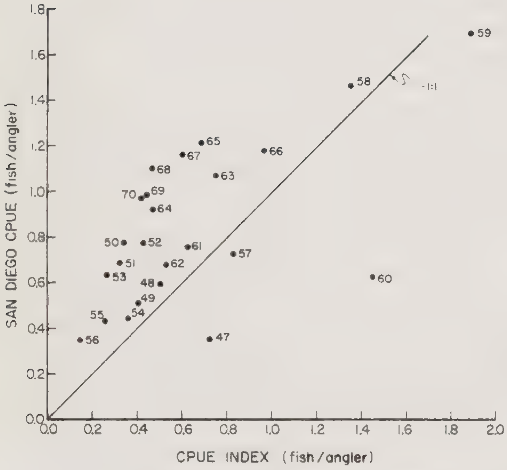

Figure 6.—Comparison of partyboat CPUE for San Diego region with CPUE index for all regions combined for California barracuda, 1947-70.

and late 1960's may not have extended fully into the southern California fishing grounds.

Since World War II the price of barracuda per pound (adjusted by the wholesale price index) paid to fishermen, has remained relatively constant (Fig. 7). The price did drop during warm water years when the supply was high. In recent years of very low supply the price has increased. As market price did not increase during the long-term decrease in landings, there was little economic incentive to maintain a fishery at the level of the early 1950's.

Stock assessment

Pinkas' (1966) study on the California barracuda utilized a Beverton and Holt dynamic pool model to investigate optimum minimum size in relation to yield per recruit. Maximum yield per recruit was estimated to occur at an age at first capture of 5 years, or approximately 28 inches minimum length. This length restriction also should have helped insure the reproductive capacity of the stock as the onset of sexual maturity occurs at age 2 for most individuals (Walford, 1932).

Commercial fishing has observed a 28-inch minimum size since the 1930's. Sport fishing has also had a 28-inch size limit but with the provision that a certain number of undersized fish could be kept (five under-sized fish from 1933 to 1957, and two under-sized fish to 1970).

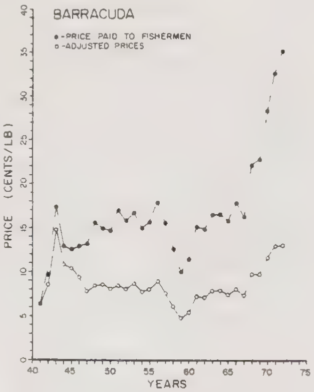

Figure 7.—Commercial ex-vessel prices for barracuda adjusted by wholesale price index, 1941-71.

Before the mid-1950's the undersize fish allowance should have had relatively little effect on yield, since the sport fishery accounted for only 30-40 percent of the total catch and large fish were presumably in abundance. By the late 1960's however, the sport fishery accounted for more than 90 percent of the landings, and fish larger than 28 inches had become relatively scarce, so that the bulk of the landings was composed of fish under 28 inches in length. In March 1971 the undersized fish allowance was abolished, making the theoretically optimum size limit effective once again.

Yield per recruit considerations, however, do not explain the observed trends in the catches, nor do they indicate the present status of the stock. In order to ascertain recent levels of exploitation with regard to catch and effort, Schaefer model analysis was attempted.

Various indices of CPUE were examined for application to the model. As previously discussed, distribution patterns have varied, with the migration not extending much north of San Diego in some years. Thus we have calculated CPUE as total annual partyboat catch of barracuda divided by total annual partyboat effort for southern California, multiplied by estimating average weight per fish to get CPUE in weight. This procedure allowed inclusion of 1936-40 partyboat catch information, which, while of relatively poor quality, provides the only "fix" on earlier levels of exploitation. Total effort is then estimated as total landings divided by CPUE. Using Gulland's approach, effort is averaged over half the fishable lifespan, hence we used 3-year averages.

As each minimum size (or characteristic length frequency) results in a different equilibrium line in the Schaefer model, the observed data points are difficult to interpret (Fig. 8). The southern California sport fishery exploits a fringe of the stock, with oceanic temperature strongly influencing availability (Radovich, 1962, 1975). Such changes in availability result in a variable relationship between nominal sport fishing effort and actual fishing mortality rate. Four groups are apparent, corresponding to different, presumably homoge-

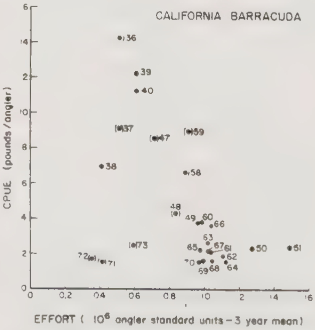

Figure 8.—California barracuda partyboat CPUE (pounds/angler) versus nominal effort (standard angler units) for 1936-73 (see text for calculation of effort for 1971-73).

neous, periods in the fishery. Data points for the late 1930's comprise a loose group included primarily for the purposes of establishing a basic relationship between catch and effort for the earlier years of the fishery. Tentative values for 1936 and 1937 are shown. Presumably an effective minimum length of 28 inches was in effect during the late 1930's (mean annual catch = 3,000 short tons). A second group, comprised of years 1947 to 1951, is characterized by declining catches (mean annual catch = 2,300 tons) and probably a minimum effective size limit of about 28 inches. The third group is composed of observations from the 1960's, a fairly stable period in effort and landings (mean annual catch = 1,200 tons), however, with an effective minimum length considerably shorter than 28 inches. The higher CPUE for 1960 may be the result of successful local spawning in previous years as suggested by the large numbers of small barracuda in the 1960 length frequency (Fig. 4).

Imposition of a strict 28-inch minimum size limit in March 1971 resulted in a sharp drop in reported partyboat catch, although the number of anglers fishing was unchanged. To adjust CPUE to pre-1971 conditions, partyboat CPUE values were increased by the ratio of total fish caught to fish of legal size (Fig. 4). This ratio was estimated from length frequency sampling done aboard partyboats. For purposes of this analysis, the length restriction resulted in decreased fishing mortality of younger fish, which takes the form of reduced "effort" in Figure 8, according to the formula: $f' = C / CPUE_{est}$, where f' is a derived measure of effort, presumably proportional to fishing mortality, C is total landings of all fisheries segments, and $CPUE_{est}$ is as described above. In this case, C is smaller than the catch used to calculate CPUE, and f' is smaller than actual number of anglers fishing. In Figure 8, the years 1971, 1972, and 1973 were thus moved to the left of the earlier group. With time, we expect to see the points progress toward the upper right, as fish landed show increasing mean weight. This should increase CPUE, and simultaneously increase the proportion of legal fish to fish caught, which will increase "effort" as it has been defined here.

Table 10.—Annual catches of Pacific bonito by main fishery segments.

	U.S. commercial			Sport					Total
Year	Calif. (10³ lb)	Mexico (10³ lb)	Mexico[1] commercial (10³ lb)	Partyboats Calif. (10³ fish)	Other Calif.[2] (10³ fish)	Mexican waters[3] (10³ fish)	Total (10³ fish)	Total (10³ lb)	Comm. and sport (10³ lb)
1950	33	662	(0)	2.4	(2.1)	(0.1)	(4.6)	(14)	(709)
1951	54	723	(0)	14.5	(13.1)	(0.8)	(28.4)	(85)	(862)
1952	8	2,135	(0)	7.6	(6.9)	(0.5)	(15.0)	(45)	(2,188)
1953	19	3,084	(0)	6.3	(5.7)	(0.5)	(12.5)	(38)	(3,141)
1954	219	2,100	(0)	70.1	(63.4)	(6.1)	(139.6)	(419)	(2,738)
1955	40	100	(0)	22.4	(20.3)	(2.2)	(44.9)	(135)	(275)
1956	22	105	(0)	61 4	(55.5)	(6.0)	(122.9)	(369)	(496)
1957	110	109	(25)	258.6	(233.7)	(30.3)	(522.6)	(1,568)	(1,812)
1958	4,805	742	(50)	422.6	(382.0)	(49.4)	(854.0)	(2,562)	(8,159)
1959	3,003	9	(75)	776.4	(701.1)	(90.8)	(1,568.3)	(4,705)	(7,792)
1960	1,220	31	(100)	1,199.9	(1,083.5)	(140.4)	(2,423.0)	(7,270)	(8,621)
1961	8,439	74	(163)	849.4	(767.0)	(119.7)	(1,736.1)	(5,208)	(13,884)
1962	2,072	63	67	798.7	(730.2)	(94.3)	(1,623.2)	(4,870)	(7,072)
1963	4,014	9	1,118	775.7	(662.4)	(91.7)	(1,529.8)	(4,589)	(9,730)
1964	2,606	6	1,125	1,298.8	(1,172.8)	(152.7)	(2,624.3)	(7,873)	(11,610)
1965	5,633	6	735	806.3	(728.1)	(96.0)	(1,630.4)	(4,891)	(11,265)
1966	18,308	840	2,044	644.4	(581.9)	(76.2)	(1,302.5)	(3,908)	(25,100)
1967	17,842	3,378	1,343	350.0	(316.0)	(42.3)	(708.3)	(2,125)	(24,688)
1968	14,903	19	779	1,102.9	(996.0)	(131.6)	(2,230.5)	(6,692)	(22,393)
1969	13,175	4,027	147	1,130.2	(1,020.6)	(139.9)	(2,290.7)	(6,872)	(24,221)
1970	8,794	399	(163)	651.9	(588.7)	(78.3)	(1,318.9)	(3,957)	(13,313)
1971	10,476	9,793	(325)	152.8	(137.8)	(16.7)	(307.3)	(922)	(21,516)
1972	15,600	6,712	(325)	419.0	(377.8)	(53.6)	(850.4)	(2,551)	(25,188)
1973	18,477	12,263	710	472.5	(426.1)	(60.5)	(959.1)	(2,877)	(34,327)

[1] Source: FAO Yearbook of Fishery Statistics, and catch data furnished by Instituto Nacional de Pesca.

[2] Estimated by Thayer (1973, table 3) less reported partyboat catch

[3] Sum of estimated Ensenada partyboat catch (est. catch = 0.117 California partyboat catch, based on mean of 1961 and 1971 reported catches, with smaller ratio for earlier years: linearly decreasing from 1958 to $^2/_5$ of ratio in 1950) and California long range partyboat catch.

Although it is possible to draw a curve through the six points from year groups one and two, such a line would probably not be a valid equilibrium curve because of the changing nature of the fishery. From the examination of the time series of catches and length frequencies, it appears that the barracuda resource was fully exploited in the late 1930's and quite heavily overexploited by the 1960's. The decline of the stock may have partly resulted from recruitment failures. The large catches during the warm water years, which were facilitated by an influx of fish into California waters, almost certainly accelerated the decline in the 1960's. It may take several years for the stock to regenerate its number from the increased spawning potential afforded by strict maintenance of a 28-inch minimum length. The unrestricted Mexican fishery and lowered survival of returned undersized fish must be expected to have dampening effects on rehabilitation of the fishery, but the end result should be an improved angler CPUE and overall yield of combined fisheries over what would be expected without the size limit.

PACIFIC BONITO

After an absence of several years, the Pacific bonito, *Sarda chiliensis*, returned in numbers in southern California waters in the latter half of 1956. Both sport and commercial fisheries presently exploit this resource virtually unchecked. Knowledge of potential sustainable yields and fisheries interactions is lacking, making an attempt at stock assessment vital.

Data

Long time series of catch statistics are available for the U.S. commerical fleet (in weight) and for the U.S. partyboats (in numbers of fish caught). Since 1961 Mexican commercial catches are regularly reported in the FAO *Yearbook of Fishery Statistics* and catches for 1962-69 and 1973 were furnished by the Instituto Nacional de Pesca (INP). For the other segments of the fishery, information is much more scanty. However, total annual catches (Table 10) were reconstructed for the period 1950-73 on the basis of specific annual catches occasionally reported for some particular segments of the fishery, general knowledge on the relative importance of respective fishery sections, and known or assumed trends in their historical development. In 1973 U.S. commercial and sport catches—with distinction made between catches taken off California and off Baja California—were regularly sampled for length frequency (Fig. 9). Length distributions for U.S. sport fishery and available weight/length relationships (Campbell, in press) were used for converting catch in numbers to weight. The conversion was done using an average weight of 3 pounds/fish (1973 partyboat average weight was 2.87 pounds), which has been the usual conversion used by CDFG. Also, the long-range partyboat catch, while taking considerably larger fish, accounts for less than 1 percent of the total catch, and does not need to be included in the calculation. Lack of length frequency information for earlier years necessitates the use of a constant mean weight estimate.

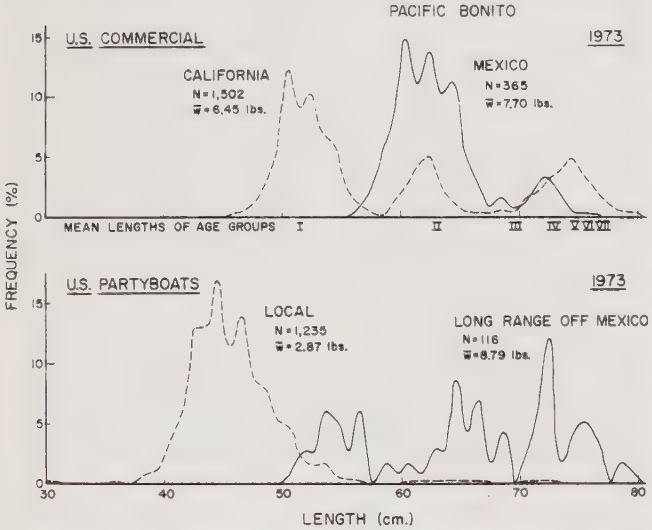

Figure 9.—Pacific bonito length frequency distributions for U.S. catches by fleet and location for 1973.

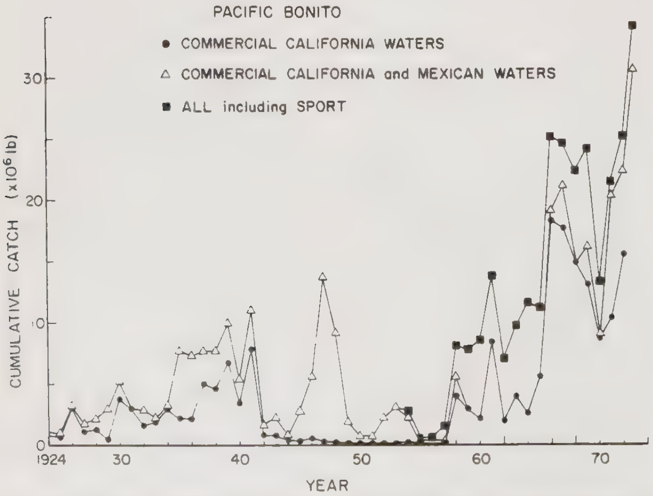

Figure 10.—Historical development of the Pacific bonito fishery: total catches of major fishery segments.

The CPUE (in numbers of fish caught per angler) data are also available for the partyboats. Source data were processed as follows:

1) Annual $\left(\frac{\Sigma C}{\Sigma f}\right)$ for all southern California areas combined.

2) Weighted mean, (or CPUE index)

$$\frac{\sum\left[a_i\left(\frac{\Sigma C}{\Sigma f}\right)_i\right]}{\Sigma a_i}$$

, with weighting factor proportional to the area (0-20 fathoms), a_i, of six respective statistical divisions (described in Table 3).

Indices of apparent abundance, derived from aerial surveys, are available for the period 1962-72 (Squire, 1972).

Trends of fishery segments

As illustrated in Figure 10, until about 1957-58, catches as a whole were at a rather low level—although showing marked oscillations. They subsequently increased in two steps. The first, from late 1950's to mid-1960's, corresponded to the development, both in Mexico and California, of sport catches. The second, beginning in the mid-1960's, corresponded to an expansion of U.S. commercial landings (Table 10).

From length frequency distributions of U.S. catches sampled in 1973 (Fig. 9), it is clear that the various fishery sections exploit different parts of the population. Such segregation in sizes caught reflects an uneven geographical distribution of various age groups. Roughly, older fish are more available offshore and in Mexico, although large fish are taken in the Santa Barbara area in the fall. The local U.S. sport fishery essentially takes individuals less than 60 cm (age 1). Long-range U.S. partyboats harvest older fish, but make a small contribution to the sport catch. Commercial vessels tend to take larger fish: 1 year old and above off California, 2 years old and above off Mexico.

Sport fishery and recruitment to commercial fishery

Indices of apparent abundance have been derived by Squire (1972) from tonnages of bonito estimated during aerial surveys (Table 11). Day and night indices have been calculated separately. Since the 1962 source data covered the last period of the year only, indices for that year were discarded in the following analyses. The aerial sur-

Table 11.—Aerial survey indices, partyboat CPUE, and correlations between various combinations of CPUE and aerial indices.

	Aerial survey		Partyboat CPUE index							
Year_i	Day index	Night index	$CPUE_i$	$CPUE_{i-1}$	$CPUE_{i-2}$	[1]$CPUE_{i-3}$	$CPUE_{i-4}$	A	B	[2]C
1963	1.71	0.85	1.53	1.63	1.73	1.87	1.20	0.95	0.65	0.38
1964	1.80	0.31	2.41	1.53	1.63	1.73	1.87	0.90	0.62	0.37
1965	1.48	0.22	1.53	2.41	1.53	1.63	1.73	1.21	0.76	0.44
1966	1.49	0.37	0.96	1.53	2.41	1.53	1.63	1.00	0.71	0.41
1967	1.03	0.49	0.50	0.96	1.53	2.41	1.53	0.71	0.53	0.34
1968	0.54	0.31	1.28	0.50	0.96	1.53	2.41	0.43	0.34	0.23
1969	0.28	0.18	1.46	1.28	0.50	0.96	1.53	0.61	0.38	0.23
1970	0.01	0.10	0.74	1.46	1.28	0.50	0.96	0.75	0.48	0.26
1971	0.56	0.21	0.23	0.74	1.46	1.28	0.50	0.54	0.41	0.24
1972	1.11	0.20	0.59	0.23	0.74	1.46	1.28	0.28	0.24	0.17
r day	—	0.58	0.50	0.39	0.60	0.69	0.26	0.56	0.64	0.71
r night	0.58	—	0.20	0.15	0.44	0.66	0.07	0.30	0.40	0.46

A: $\sum_{j=1}^{4} CPUE_{i-j}e^{-j}$

B: $\frac{1}{2} CPUE_{i-1}e^{-1} + \sum_{j=2}^{4} CPUE_{i-j}e^{-j}$

C. $\frac{1}{4} CPUE_{i-1}e^{-1} + \frac{1}{2} CPUE_{i-2}e^{-2} + \sum_{j=3}^{4} CPUE_{i-j}e^{-j}$

[1]These are plotted in Figure 3
[2]These are plotted in Figure 4

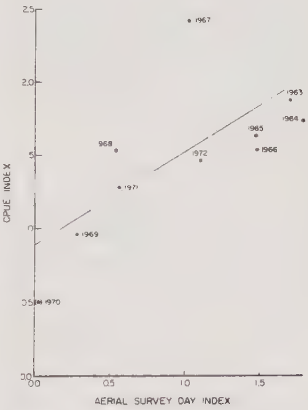

Figure 11.—Regression of aerial survey day index against partyboat CPUE index 3 years earlier.

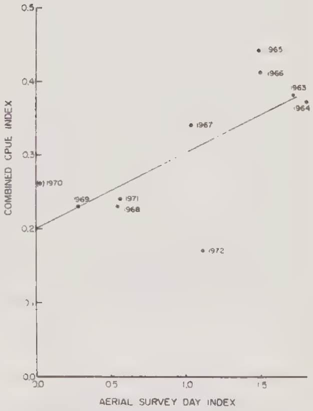

Figure 12.—Regression of aerial survey day index against CPUE adjusted for mortality and recruitment.

vey indices have been recalculated to exclude the area north of Pt. Conception in order to correspond with other biomass estimates, particularly southern California partyboat CPUE for bonito.

A number of correlations between aerial survey indices and partyboat CPUE—with various yearly lag times and combination—were calculated (Table 11). Highest values of the correlation coefficient (*r*) were found with indices derived from daytime observations. Squire (1972) felt that daytime aerial observations were more efficient than night observations for estimating bonito abundance. The highest correlation was observed between partyboat CPUE and daytime aerial index 3 years later (Fig. 11). Taking into account age composition of catches made by sport and commercial fisheries respectively (Fig. 9) and the fact that airplanes are mainly assisting the commercial fishery and therefore likely concentrate their surveys over commercial fishing grounds, it is reasonable to assume that aerial surveys mainly reflect changes occurring in that part of the bonito stock exploited by commercial vessels, while partyboat CPUE provides an index of prerecruit abundance before they start to be exploited by the commercial fleet. However, there is not an exact 3-year lag in age composition of partyboat and commercial catches. Moreover, while partyboats may essentially exploit a single age group, commercial vessels exploit several age groups. In order to account for mortality, plus selectivity by commercial fishing, various reasonable combinations of partyboat CPUE (in numbers) over years were tentatively correlated with daytime aerial survey indices. The highest correlation (r = 0.71) was found for the combination:

$$\text{Day AI}_i \propto \tfrac{1}{4}\, CPUE_{i-1}e^{-1} + \tfrac{1}{2} CPUE_{i-2}\, e^{-2} + \sum_{j=3}^{4} CPUE_{i-j}e^{-j}$$

(Fig. 12).

(A value of 1.0 was arbitrarily used for *Z*.) This formula attempts to relate abundance as measured by the daytime aerial index (day AI) to the history of recruitment as measured by partyboat CPUE index values. The CPUE's were multiplied by coefficients to account for mortality and recruitment (25 percent and 50 percent were used for the younger age groups).

Although 1973 length frequency samples from the partyboat catch are dominated by a single age group, this may not have been the case in earlier years. Consequently, partyboat CPUE may reflect the spectrum of age groups available to the commercial fishery (or more precisely, the aerial index) 3 years later rather than reflect the recruitment strength of a single year class as suggested by the 1973 frequencies. In either case, partyboat CPUE appears to be a valid indicator of recruitment to the commercially exploitable phase for recent years. The history of CPUE values (Fig. 13) indicates recruitment, from presumably local spawning, was very low before 1957, after which it sharply increased.

Annual catches of 1,000-4,000 tons of bonito were taken commercially from California waters between 1926 and 1941, but information on the effort required to make those catches is lacking. Between 1942 and 1957 annual catches were very low, never exceeding 500 tons and often below 50 tons. Partyboat CPUE of bonito was low before 1956. Reporting of bonito-like species by partyboats was fairly good (Pacific mackerel, 90 percent; "other species," 68 percent) in the period 1947-51 (Baxter and Young, 1953). During the 1920's and 1930's, bonito were commonly caught from fishing piers along the coast and from fishing barges anchored offshore (J. Radovich, pers. commun.).

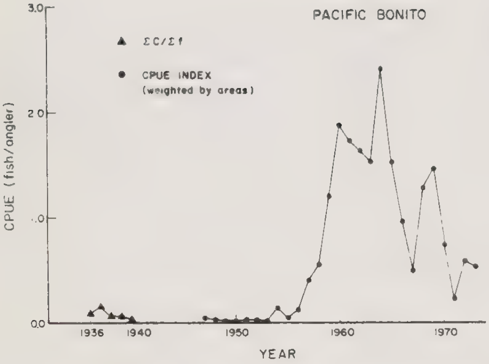

Figure 13.—Partyboat CPUE (in numbers) as an index of annual recruitment.

For unknown reasons, bonito became scarce sometime during the early 1940's. This disappearance of the resource was independent of fishing, which was curtailed during World War II. Subsequently, bonito catches on partyboats were dependent on migratory fish until 1956, when large quantities of bonito moved into California waters and became reestablished as a locally spawning population. Management of the resource will assume different forms according to whether the resource is migratory or permanent. It is here assumed that the resource is sufficiently permanent to attempt management on the basis of sustainable yield. Nonetheless, there is no evidence that residency is other than a temporary event.

Stock assessment

The present state of the bonito resource has been assessed using total catch and a combination of partyboat CPUE and aerial survey data index for the years 1963 through 1972. Previous discussions suggested that aerial survey data index has some validity as a measure of apparent abundance of the biomass exploited by commercial boats, and similarly partyboat CPUE index is probably proportional to biomass exploited by sportsmen. Since sport and commercial fisheries exploit different age groups and commercial effort data do not exist, a combination of the above two indices provides the only means for stock evaluation using a surplus production model.

The combined index for each year was an average of the two indices standardized by their respective means for the 10-year time series (excluding 1970) and weighted by their respective annual catches (Table 12). The ratio of total catch (C) to this mean index should vary in relation to fishing effort $\left(\frac{\text{Catch}}{\text{Index}} \propto \frac{C}{B} = K\right)$. The units of measurement for this ratio or f are abstract. The mean index for biomass (B) and total catch were plotted against the effort index (Fig. 14). In order to take into consideration the average duration of the exploited phase (slightly above 4 years), the effort index was averaged for 2 successive years. The biomass index decreases with increasing effort in a nearly linear fashion. The relationship does suggest a concave upward curve, but this has little effect on conclusions. The sudden increase in commercial catch in 1966 apparently was greater than equilibrium level as would be expected from large-scale fishing of a previously unexploited stock. However, for the level of recruitment since 1960, the stock appears to be intensively exploited. In fact, the 1973 catch of 34 million pounds apparently is substantially above the MSY suggested by the analysis. Given that recent partyboat CPUE values do not indicate any strong year classes in the present population, this high catch may prove to be disastrous to the bonito stock. Determination of equilibrium abundance and yields are confounded by a possibly density-independent decrease in recruitment, highly variable availability due to behavioral changes (Collins, CDFG[5]) and generally low precision and coverage of available data. Nonetheless it appears likely that fisheries take an appreciable share of each year class.

Table 12.—Index of exploited biomass, total catch, and calculated effort for Pacific bonito, 1963 to 1972.

Year	Aerial survey day index	Comm landings 10³ lb	Partyboat CPUE index	Sport catch 10³ lb	Weighted mean index	Total catch 10³ lb	Effort index (10³)	Effort index 2-year mean (10³)
1963	1 71	5.141	1.53	4,589	1.43	9,730	6,782	—
1964	1 80	3.737	2.41	7.873	1.93	11,610	6,031	6.406
1965	1 48	6.374	1 53	4.891	1.33	11.265	8.496	7 264
1966	1 49	21.192	0.96	3.908	1.26	25.100	19.860	14.178
1967	1 03	22.563	0.50	2,125	0.89	24 688	27.843	23.852
1968	0.54	15.701	1 28	6.692	0.67	22.393	33.424	30.634
1969	0.28	17 349	1 46	6.872	0.54	24.221	45.152	39 288
1970	0 01	9.356	0.74	3.957	—[1]	13.313	—	—
1971	0 56	20 594	0.23	982	0.49	21 576	43.900	—
1972	1 11	22.637	0 59	2.551	0 95	25.188	26.464	35.182

Aerial survey data for 1970 incomplete

In the absence of information on mortality rates (or even comparative mortality rates for similar species) yield per recruit analysis was not attempted. Moreover, lack of mortality rate estimates preclude analysis of the interaction between sport catch and commercial yield or rates of exploitation. Comparison of numbers of fish caught by sport and commercial vessels respectively (Table 13), and observations made above suggest that the sport rate of exploitation is relatively low. However, expansion of the sport fishery will directly affect the recruitment to the phase exploited by commercial vessels and consequently affect their catches.

Expansion of commercial activities will not directly affect the sport fishery, which exploits younger fish. However, decrease in sport CPUE could result from a reduction of parental stock to a point where recruitment is significantly reduced. Up to now this has most likely not occurred; however, the 1973 fishing season appears to have been considerably in excess of equilibrium yield and may have severely affected the resource. Although such events cannot be neglected, their occurrence is very difficult to determine for a stock subject to large natural fluctuations in recruitment, as is the Pacific bonito.

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[5] R. Collins, CDFG, 350 Golden Shores, Long Beach, CA 90802. Pers. commun

JACK MACKEREL

The jack mackerel, *Trachurus symmetricus* (Ayres), fishery has been one of the mainstays of the southern California wetfish fleet since the decline of the Pacific sardine. On rare occasions large sport catches are made but jack mackerel remains primarily of commercial interest.

Catches

Long time series of landings in weight are available for the main segments of the fishery: California cannery landings, Mexican cannery landings, and California live bait landings (Table 14). A similar time series in numbers of fish landed is available for the California partyboat fishery, and landings for other sport fisheries were estimated by means of a simple ratio to partyboat landings (3.0 fish/partyboat fish). Sport-caught fish were arbitrarily assigned a weight of 1 pound apiece in the calculation of total landings. In the year of largest sport landings, 1953, sport-caught fish comprised only 1.3 percent of total landings, and the percentage for most years falls far below this value.

Commercial landings have been strongly influenced by the availability of more lucrative species. Landings during the 1950's tend to be inversely related to sardine availability. The slight decline

Table 13.—Pacific bonito—number of fish caught (in thousands) by commercial fleets and sport fishery.

	Commercial				
	U.S.				
Year	Calif.	Mexico	Mexico	Total	Sport total
1950	5	86	0	91	5
1951	8	94	0	102	28
1952	1	277	0	278	15
1953	3	401	0	404	13
1954	34	273	0	307	140
1955	6	13	0	19	45
1956	3	14	0	17	123
1957	17	14	3	34	523
1958	745	96	6	847	854
1959	466	1	10	477	1,568
1960	189	4	13	206	2,423
1961	1,308	10	1	1,319	1,736
1962	321	8	9	338	1,623
1963	622	1	90	713	1,530
1964	404	1	146	551	2,624
1965	873	1	95	969	1,630
1966	2,838	109	266	3,213	1,303
1967	2,766	439	174	3,379	708
1968	2,311	2	101	2,414	2,231
1969	2,043	523	18	2 584	2,291
1970	1,363	52	21	1,436	1,319
1971	1,624	1,272	42	2,938	307
1972	2,419	872	42	3,333	850
1973	2,685	1,593	92	4,370	959

Table 14.—Catches of jack mackerel for various fisheries

	Commercial			Sport			
	United States						
Year	Cannery 10³ lb	Bait 10³ lb	Mexico cannery 10³ lb	Partyboat California 10³ fish	All other California plus Mexico[3] 10³ fish	Total sport 10³ lb[4]	Total commercial and sport 10³ lb
1950	133,255.8	0.4	[1](7,000)	0.6	(1.8)	(2.4)	(140,259)
1951	89,838.1	0.0	(4,000)	0.2	(0.6)	(0.8)	(93,839)
1952	146,521.7	33.1	(3,000)	4.4	(13.2)	(17.6)	(149,572)
1953	55,750.9	1.4	(3,000)	196.3	(588.9)	(785.2)	(59,538)
1954	17,333.6	0.4	440	19.4	(58.2)	(77.6)	(17,852)
1955	35,754.7	0.0	13,300	39.5	(118.5)	(158.0)	(49,213)
1956	75,762.1	0.0	14,200	23.5	(70.5)	(94.0)	(90,056)
1957	82,011.8	0.0	[1](8,000)	6.9	(20.7)	(27.6)	(90,039)
1958	22,065.8	6.2	(2,000)	27.9	(83.7)	(111.6)	(24,184)
1959	37,507.2	40.0	(500)	11.8	(35.4)	(47.2)	(38,094)
1960	74,945.5	4.0	(5,000)	8.5	(25.5)	(34.0)	(79,984)
1961	97,606.3	0.0	3,934	28.9	(86.7)	(115.6)	(101,656)
1962	89,978.9	0.0	6,978	9.0	(27.0)	(36.0)	(96,993)
1963	95,442.3	15.0	30,153	9.3	(27.9)	(37.2)	(125,648)
1964	89,692.9	0.0	6,871	6.6	(19.8)	(26.4)	(96,590)
1965	66,666.4	0.0	8,420	25.6	(76.8)	(102.4)	(75,189)
1966	40,862.4	25.0	12,919	19.0	(57.0)	(76.0)	(53,882)
1967	38,180.5	0.0	4,285	16.2	(48.6)	(64.8)	(42,530)
1968	55,667.7	158.0	3,549	13.6	(40.8)	(54.4)	(59,429)
1969	51,921.2	103.0	3,336	11.3	(33.9)	(45.2)	(55,405)
1970	47,746.5	0.0	[2](5,000)	15.7	(47.1)	(62.8)	(52,809)
1971	59,883.0	9.0	(5,000)	10.6	(31.8)	(42.4)	(64,934)
1972	51,117.6	5.0	(5,000)	5.9	(17.7)	(23.6)	(56,146)
1973	20,615.8		438	15.8	(47.4)	(63.2)	(21,117)

[1] Estimated from reported catch of Pacific and jack mackerel combined.
[2] Information not available—rough maximal estimate.
[3] Estimated as partyboat catch × 3.0.
[4] Estimated from assumed weight of 1 pound per fish.

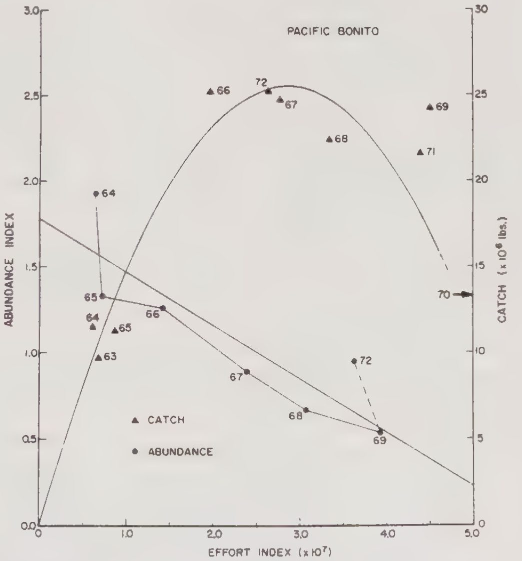

Figure 14.—Relationship between combined CPUE and effort and the corresponding estimates of surplus production for Pacific bonito.

Table 15.—Indices and estimates of biomass.

Year	Larvae CalCOFI area[1] (10^9)	Aerial survey index		Biomass estimate 10^6 tons	
		Night	Day		
1950	6.846				
1951	4 233				
1952	3.921				
1953	1.484				
1954	2,413				
1955	2,635			0.35	(Spawning biomass, local area based on eggs and larvae[2])
1956	1,372				
1957	2,876				
1958	830				
1959	545				
1960	655				
1961	981				
1962	2.516				
1963	3,122	2.98	1.41		
1964	3,045	2.18	1.62	1.4-2.2	(Spawning biomass, CalCOFI area based on eggs and larvae[3])
1965	2.681	1.36	0.71		
1966	6.288	1.94	0.28		
1967		1.41	0.20		
1968		2.25	0.30		
1969		0.65	0.11		
1970		0.58	0.16		
1971		0.92	0.04		—
1972		0.74	0.13	0.7-1.5	(Exploited biomass, based on tagging[4])

[1] Uncorrected for temperature. 1957-59 are probably underestimated

[2] MacGregor (1964)

[3] Ahlstrom (1968)

[4] Knaggs (1973)

in landings since 1965 has been primarily due to expansion of fisheries on the Pacific bonito and on the northern anchovy.

Status of the stock and its exploitation

Aged landings of jack mackerel were not completed in time to be included in this report; however, they are now available (Knaggs, 1974 and Knaggs and Barnett, 1975). This information will afford an opportunity for detailed analysis of the fishery by use of cohort analysis (Murphy method); the present discussion is restricted to very simple and general terms.

Various indices of abundance (Table 15) show that the resource tends to be highly variable in magnitude and egg-and-larva surveys show the stock to be extremely widespread. Ahlstrom (1968) estimated the spawning biomass in the CalCOFI region to have been between 1.4 and 2.4 × 10^6 tons, based on egg and larval occurrences in 1964-66. Knaggs (1973) estimated from tag returns that between 0.7 and 1.5 × 10^6 tons were available to the fishery in 1972. These estimates are in agreement with trends in the aerial survey index (Squire, 1972). This suggests that jack mackerel are now about half as abundant as they were in the mid-1960's. However, egg-and-larva estimates of spawning biomass do not necessarily correspond to exploitable biomass. Juveniles are exploited, while old fish emigrate from the fishing grounds.

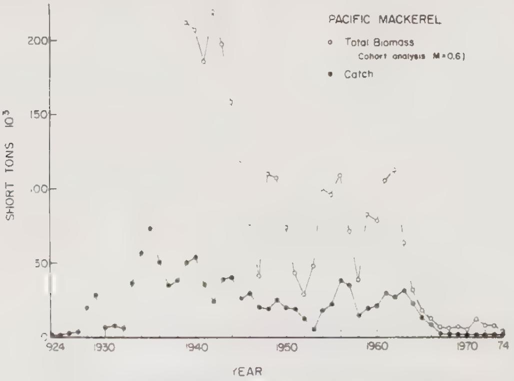

Figure 15.—Pacific mackerel annual catches and biomass estimates.

The present level of fishing is very low, with an *F* of 0.02-0.04 (Table 16), indicating that the yield could be increased manyfold. Application of Gulland's quick calculation of potential yield ($Y_{pot} = 0.5 \times M \times B_0$) gives 210,000 to 450,000 tons, assuming $M = 0.6$ and using the 1972 estimates of biomass, B_0. Yield values will vary according to the biomass, and would be proportionately larger if the stock were at the 1964-66 level of abundance.

There are indications that estimation of MSY may not be so simple. Knaggs and Barnett (1975) have noted a decrease in average age of the catch, which suggests the possibility of a much higher total mortality rate or smaller stock size than generally believed. Fishermen are of the opinion that jack mackerel abundance has decreased considerably (E. Knaggs, pers. commun.). Comparative biology and exploitation of similar *Trachurus* species and detailed analysis of aged landing data may resolve this dilemma of response of the California stock to apparently very low fishing mortality.

PACIFIC MACKEREL

Inception of Pacific mackerel, *Scomber japonicus*, canning in the late 1920's caused a sudden rise in landings, which, augmented by what was the strongest year class (1932) in the documented history of the fishery, peaked at a record 146 million pounds in the 1935-36 season. Subsequently, the catches went through a long, fluctuating decline, ending with a severely depleted stock in 1933 (Fig. 15). However the 1953 spawning was highly successful, leading to a resurgence of the stock and the fishery, which remained healthy throughout the decade. Beginning in 1963, a sequence of six exceptionally severe recruitment failures resulted in extinction of the commercial fishery.

The Pacific mackerel remains a rather popular and sufficiently abundant target of sport fishermen, although lacking the esteem given to the larger game fish.

Exploitation and dynamics

The Pacific mackerel has been subject to severe and rather unpredictable fluctuations in recruitment, although a 6-year cyclic pattern has been described. Parrish (1974) showed that the fishery has depended largely upon occa-

Table 16.—Biomass, catches, and fishing mortality of jack mackerel.

Years	Biomass (10^6 tons)	Catch (10^3 tons)[1]	$F = C/B$
1964-66	1.4-2.2	37.3	0.02-0.03
1972	0.7-1.5	28.1	0.02-0 04

[1] 3-yr average

sional strong year classes and has tended to overexploit successive weak year classes. As the spawning biomass was reduced, variance in spawning success increased, augmenting the dependency on strong year classes, while reducing the mean age and number of age classes in the population to a point where the stock could not withstand an extended period of recruitment failure. However, intensive fishing is probably not the only cause responsible for such collapse.

As for most stocks where similar events were experienced, the respective roles of natural causes and of those due to fishing have not been satisfactorily explained. Long-term fluctuations in the environment and the species composition of the southern California pelagic community have been observed since the late 1950's and early 1960's, e.g., waters generally warmer than during the previous decade, progressive predominance of anchovy over the sardine, and reestablishment of a local population of Pacific bonito, a likely competitor with the Pacific mackerel.

Management

In response to the collapse of the stock a moratorium on commercial fishing was adopted in 1970. Later, a more comprehensive management bill was passed by the California legislature which provides for the rehabilitation and subsequent regulation of a sustained and controlled commercial fishery should the stock recover and increase over a minimum biomass. In essence, the law provides for a harvest equivalent to 20 percent of the spawning biomass in excess of 10,000 tons and to 30 percent of the spawning biomass above 20,000 tons. The closure of the commercial fishery for spawning biomass below 10,000 tons—the present situation—aims at ensuring that a minimum parental stock is maintained and a minimum sport fishing stock is provided.

Above the 10,000-ton and 20,000-ton thresholds, the adopted regulation ensures that the maximum amount of fishing is controlled and that it will gradually increase, tending towards an asymptote of $F = 0.3$ as the stock gains in size.

Direct limitation of effort would achieve the same effect of limiting F, without the difficulties and costs inherent in forecasting recruitment and subsequent fishable biomass. This aspect is particularly relevant to the Pacific mackerel stock, which has shown fluctuations of large amplitude. However the practical difficulties involved in implementing management based on effort limitation may well counterbalance its previously mentioned advantages. In that respect it should also be noted that while quota limitation alone is insufficient to prevent economic overfishing, enforcement of quotas adjusted on early estimates of the recruits should dampen year-to-year oscillations in the fishable biomass and thus provide the fishery with greater stability than was had previously.

Present state of exploitation and perspectives

As a result of the above restrictions on commercial fishing, sport fishing is presently the largest user of Pacific mackerel in California (Table 17). Fishing mortality is at present low ($F = 0.06$), indicating that it is not necessary to implement further restrictions on the sport fishery.

Recovery of the stock to commercial viability is now largely a matter of fortune, as the spawning biomass is so small that local environmental fluctuations may have a large influence on spawning success. Moreover, potential response of the stock in the present environmental regime is unknown. Based on knowledge of present biomass and recent recruitment, it is unlikely that a fishery will develop in the next 5 years.

PACIFIC SARDINE

The purpose of this report on Pacific sardine, *Sardinops caeruleus*, is not to discuss the population dynamics of the stock but only to document the total biomass time series. The southern California spawning biomass of Pacific sardine may presently be less than 5,000 tons (P. Smith, National Marine Fisheries Service, (NMFS), pers. commun.), and a moratorium on fishing is in effect. Accordingly, no further attempt is made to determine the status of the stock.

We are interested though in the sardine stocks because, along with anchovies, they make up a major portion of the forage for many of the southern California sport fishes. Also, the present wetfish fleet is the remnant of the sardine purse seine fleet. During the collapse of the sardine fishery the fishermen began redirecting their effort towards other pelagic species, including Pacific mackerel, jack mackerel, and later, anchovy and bonito. The response of the sardine resource to fishing pressure is now mainly of academic interest and is discussed by Clark and Marr (1955) and Murphy (1966).

Various indices of biomass reflect the tremendous decline in the stock from 1.3 million tons in 1940 to the 2,000-5,000 tons at present (Table 18, Fig. 16). Sardine biomass combined with anchovy biomass estimates show an interesting cycle with the lowest amount at 1 million tons in 1950 increasing to over 6 million tons by 1961 (Fig. 16). Combined forage fish biomass has increased 6-7 fold since its low in 1950.

Such cycles in biomass are apparently common events in history as demonstrated by occurrence of fish scales in ocean bottom sediments examined by Soutar and Isaacs (1974). Their work suggests that for the Santa Barbara Basin the level of anchovy stock over the past 150 years has been relatively constant. The level since about 1920, though, appears to be below average

Table 17.—Recent biomass, catches, and fishing mortality rates of Pacific mackerel.

Year	Biomass[1]		Sport catch[2]		Commercial catch		Total catch 10^3 lb	$F = C/B$
	Spawning 10^3 lb	Total 10^3 lb	Number 10^3	Weight[3] 10^3 lb	Calif. 10^3 lb	Mexico 10^3 lb		
1972	10,000	15,772	495.1	415.9	108.0	(400)	924	0.06
1973	11,000	15,224	376.5	425.4	56.7	438	920	0.06

[1] Knaggs, CDFG, pers. commun

[2] Estimated from known partyboat and barge catches, all other sport estimated as 0.826 partyboat catch.

[3] Weight conversions: 1972—0.84 pounds/fish, 1973—1.13 pounds/fish, based on 1970 year class

Table 18.—Biomass estimates: anchovy and sardine (After P. Smith, 1972, Table 12 and Figure 13).

Year	Ratio anchovy spawner biomass (10^3t)	Regression anchovy spawner biomass (10^3t)	Mean (1,2)	Murphy sardine spawner biomass (10^3t)	Regression sardine spawner biomass (10^3t)	Mean (4,5)	Anchovy and sardine spawner biomass (3+6)
	(1)	(2)	(3)	(4)	(5)	(6)	
1940	2,359		2,359	1 296		1,296	3,655
1941	2,871		2,871	2,001		2,001	4,872
1942				1,913		1,913	
1943				1,647		1,647	
1944				1,142		1,142	
1945				691		691	
1946				412		412	
1947				387		387	
1948				524		524	
1949				682		682	
1950	279		279	716		716	995
1951	690	637	664	570	553	562	1,226
1952	856	797	827	554	542	548	1,375
1953	(1,404)	1,335	1,370	709	450	1,159	2,529
1954	1,937	1,816	1,877	668	658	1,326	3,203
1955	1,855	1,676	1,766	425	404	829	2,595
1956	1,307	1,491	1,399	293	351	322	1,721
1957	1,869	1,964	1,917	212	234	223	2,140
1958	2,875	2,771	2,823	281	299	290	3,113
1959	(2,418)	2,299	2,359	190	117	154	2,513
1960		3,079	3,079		201	201	3,280
1961		3,189	3,189		132	132	3,321
1962		6,248	6,248		151	151	6,399
1963		6,030	6,030		78	78	6,108
1964		5,121	5,121		104	104	5,225
1965		7,771	7,771		226	226	7,997
1966		5,116	5,116		151	151	5,267
1967		—	—		—	—	—
1968		(2,167)	(2,167)		—	—	—
1969		(3,378)	(3,378)		27	27	3,405
1970					—	—	
1971					2-5	2-5	

Table 19.—White seabass—catches by year and by main fishery segments.

	Commercial (10^3 lb)			Sport (10^3 Fish)					
	U.S.								
Year	Calif.	Mexico	Mexico	Party-boats Calif. waters	Other open water (U.S., Mex.) est.[3]	Shore-line, pier, jetty, bay est.[4]	Total sport catch	Total sport catch (10^3 lb)	Est. total catch (10^3 lb)
1950	1,123	408	[1](74)	54.7	4.7	(9.0)	(68.4)	(532)	(2,137)
1951	955	578	(74)	44.4	5.2	(9.0)	(58.6)	(445)	(2,052)
1952	692	455	(74)	41.0	6.0	(9.0)	(56.0)	(423)	(1,644)
1953	471	402	(74)	28.2	5.8	(9.0)	(43.0)	(288)	(1,235)
1954	434	772	(74)	41.6	7.9	(9.0)	(58.5)	(445)	(1,725)
1955	545	370	(74)	30.1	7.6	(9.0)	(46.6)	(341)	(1,330)
1956	414	667	(74)	19.8	7.1	(9.0)	(35.9)	(246)	(1,401)
1957	1,262	245	(74)	19.0	7.5	(9.0)	(35.5)	(243)	(1,824)
1958	2,751	99	(74)	34.0	10.2	(9.0)	(53.2)	(398)	(3,322)
1959	3,386	38	(74)	10.6	6.7	(9.0)	(26.3)	(161)	(3,659)
1960	1,087	149	(74)	15.7	7.7	(9.0)	(32.4)	(215)	(1,525)
1961	458	236	(74)	14.1	7.5	(9.0)	(30.6)	(199)	(967)
1962	209	366	158	14.6	7.8	(9.0)	(31.4)	(125)	(858)
1963	372	519	47	19.8	9.0	(9.0)	(37.8)	(262)	(1,200)
1964	551	840	82	14.9	8.1	(9.0)	(32.0)	(211)	(1,684)
1965	578	851	87	9.8	7.1	(9.0)	(25.9)	(157)	(1,673)
1966	675	663	69	4.0	5.6	(9.0)	(18.6)	(93)	(1,500)
1967	508	715	36	3.4	5.5	(9.0)	(17.9)	(87)	(1,346)
1968	210	652	18	4.1	5.7	(9.0)	(18.8)	(95)	(975)
1969	251	848	93	4.1	5.8	(9.0)	(18.9)	(94)	(1,286)
1970	426	675	(92)	4.4	6.5	(9.0)	(19.9)	(98)	(1,291)
1971	552	272	(82)	5.3	6.5	(9.0)	(20.8)	(164)	(1,050)
1972	548	227	[2](157)	3.9	5.7	(9.0)	(18.6)	(133)	(1,065)
1973	581	228	(100)	7.1	7.0	(9.0)	(23.1)	(130)	(1,039)

[1] 1950-1961 catches estimated as 1962-1969 mean, other Mexican data courtesy of Instituto Nacional de Pesca.

[2] Preliminary estimate based on information through September and mean catches for October, November, and December

[3] Includes long-range partyboats, private boats (linear interpolation: 1964—0 225 partyboat catch, 1950—0.05 partyboat catch) and Mexican partyboats (linear interpolation: 1971 catch = 4,338, 1961 catch = 4,901 1950-1956 increasing from 2,000)

[4] 1963 pier and jetty catch = 8,551 (Pinkas et al., 1967), 1965-66 shoreline catch = 699 (Pinkas et al. 1968)

(Fig. 17). During the same period the sediments reveal cyclic occurrences of sardines. Sardines probably peaked during 1854 to 1864, 1889 to 1899, and 1914 to 1924 (Fig. 17). Just prior to the decade of 1870, sardines apparently declined to a very low level but the stock had rebounded by 1890. During the last 150 years sardine scale deposits only exceeded those of the anchovies in four 5-year periods. Scale deposition rate for anchovies, however, seems to be higher per unit of biomass than for sardines. Despite this, it seems that, on the average, the anchovy biomass has exceeded that of the sardine. Therefore, since anchovies may usually be the dominant species, if the sardine stock does rebuild, it should not be expected to overweigh, on the average, that of the anchovy.

WHITE SEABASS

The white seabass, *Cynoscion nobilis*, is one of the most highly esteemed game fishes found in southern California waters, both in the catching and in the eating. Accordingly, it commands a high market price. Recent conflicting trends in indices of apparent abundance or availability have given rise to concern over the status of the stock. This study attempts, with the limited information available, to assess the present condition of the stock, interactions between the fisheries seg-

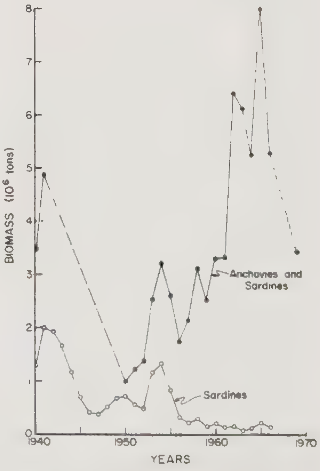

Figure 16.—Combined spawning biomass of anchovies and sardines for years 1940-69.

ments, and the possible effects of various management alternatives.

Data available

Catch and CPUE data available for the various fishery segments suffer from similar limitations as described for other sport species. Long time series of catch statistics are available for fleets responsible for the bulk of total catches, i.e., the U.S. and Mexican commercial fisheries (only since 1966 for the latter). Annual numbers of fish caught by partyboats have also been regularly reported for the whole period under review. For the other sectors, quantitative information is only available for a few occasional years. On the basis of such information and on known or assumed trends in the history of their respective developments, annual catches have been reconstructed for insufficiently documented fishery sections. Assumptions made are given in footnotes on Table 19. Catches in numbers of fish have been converted to catches in weight using the following mean weights of fish caught by fishery sectors: 8.8 pounds when one or two undersized fish can be kept and 16.9 pounds when no fish under 28 inches can be kept. Since unreported catches represent only a small percentage of total catches in weight (e.g., 5, 5, 6, and 11 percent in 1968, 1969, 1970, and 1971, respectively) estimated total catches should not depart significantly from actual figures.

The CPUE data for white seabass are available for the period considered for U.S. commercial fishery in units of:

1) Pounds of fish/boat; 2) pounds of fish/boat landing more than 1 ton during the year; 3) pounds landed/boat landing.

The CPUE for the U.S. partyboat fishery is calculated in units of numbers of fish/angler weighted by the surface area of six geographical subareas, i.e., CPUE index.

These data are summarized in Table 20 and in Figure 18.

Historical trends in annual catches and CPUE

Information presented in Figure 18 shows that total white seabass catches have decreased during the period under review, i.e., from 1950 to 1972. If year-to-year fluctuations in fishing activity,

Table 20.—White seabass—CPUE available for the commercial fishery[1] and for the partyboats and estimated total effort derived from estimated total catch (Table 19) and commercial CPUE (pounds/boat with catches > 1 ton).

Year	Commercial lb/boat	Commercial lb/boat (C > 1 ton)	Pounds landing	Partyboats fish/angler day[2]	Estimated Total effort standard unit[3]
1947	—	—	—	0.0428	—
1948	—	—	—	0.0451	—
1949	—	—	—	0.0654	—
1950	—	—	—	0.0603	—
1951	5,476	16,973	435	0.0486	123.2
1952	4,498	9,369	380	0.0585	179.6
1953	4,456	6,417	501	0.0360	201.7
1954	6,348	16,243	751	0.0533	108.6
1955	4,597	8,081	484	0.0516	169.4
1956	7,508	16,689	772	0.0314	86.3
1957	5,057	11,491	417	0.0243	162.1
1958	6,521	23,712	572	0.0547	141.7
1959	13,916	29,918	552	0.0170	123.6
1960	7,631	12,136	293	0.0340	128.9
1961	4,157	7,074	278	0.0264	142.2
1962	3,779	7,102	340	0.0388	125.7
1963	6,232	11,033	377	0.0493	114.7
1964	8,917	19,405	633	0.0340	88.4
1965	10,274	18,199	567	0.0196	93.4
1966	10,213	16,738	473	0.0089	92.6
1967	8,734	16,284	556	0.0066	87.0
1968	6,113	14,606	578	0.0060	69.3
1969	9,391	19,294	844	0.0068	69.9
1970	8,408	17,839	794	0.0049	75.2
1971	6,242	13,426	409	0.0109	80.1
1972	5,015	10,818	394	0.0065	106.5
1973	—	—	—	0.0087	—

[1] Commercial effort information courtesy of R. Collins and C. Hooker, CDFG.
[2] Based on angler CPUE index as described in text.
[3] Standard unit is boat ($C > 1$ ton).

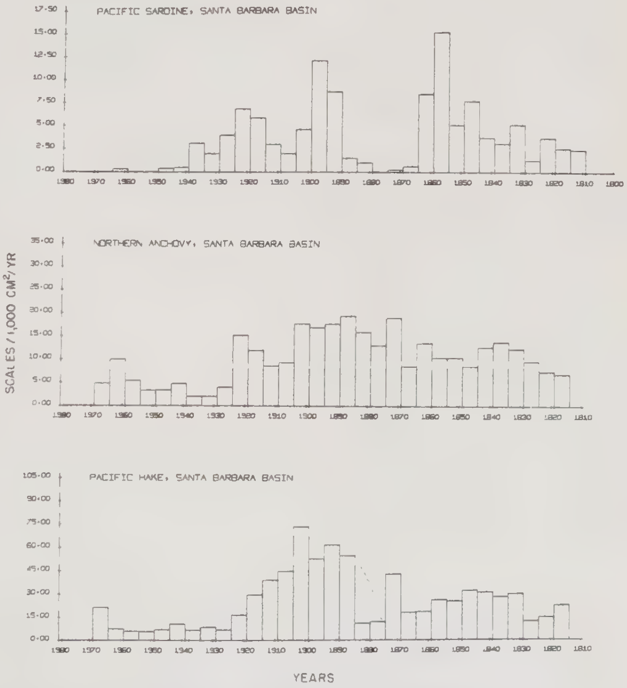

Figure 17.—Histogram plot of the scale-deposition rate of the Pacific sardine, the northern anchovy, and the Pacific hake in sediment of Santa Barbara Basin, 1810-1969 (from Soutar and Isaacs, 1974).

recruitment, and availability (in particular the sudden increase observed in 1958-59 and said to be associated with exceptionally warm waters) are neglected, total catches regularly decreased by 42.5 percent from 1950 to 1972. This drop is essentially due to the reduction in activity of the U.S. commercial fishery, the landings of which have dropped by some 50 percent during the same period. The Mexican commercial fishery is believed to have remained fairly stable during the whole period. Catches of the U.S. sport fishery and particulary of partyboats have also regularly decreased during the whole period. Although smaller in absolute terms than the decline experienced in the commercial fishery, catches of partyboats have shown a drop of almost 90 percent during the last two decades.

Although the overall partyboat CPUE of white seabass has also decreased by approximately the same amount as the catch during this period, the drop in annual catch and CPUE for partyboats cannot be explained by a general reduction in stock abundance related to fishing activity of the various fishery sections unless the catchability coefficient, *q*, is positively correlated with population size. The positive trend in U.S. commercial fishery CPUE, which has seen an average increase of 27 percent between 1951 and 1972, suggests *q* for the commercial fishery may be negatively correlated with population size. The most likely explanation for the opposite trends in CPUE of partyboats and commercial vessels is that the *q*'s for the two fisheries are nonlinear and oppositely (or at least differently) related to population size.

Total stock appraisal

A preliminary assessment of white seabass was made from overall annual catches (Table 20) and commercial fishery CPUE (pounds/boat with annual landings > 1 ton). For that purpose, Gulland's (1969) approximation method has been used. The CPUE figures were plotted against average effort during the 5 previous years (average duration of exploited phase = 9-10 years). Fishing power has probably not increased substantially since the early 1950's as boats have remained fishing about the same amount of gear. Introduction of nylon net material may have had some effect on fishing power (R. Collins and C. Hooker, CDFG, pers. commun.). The 1958 and 1959 values have been deleted in the fitting because of abnormally high catches. Subsequent CPUE observed during these years were most likely due to above-average availability of the stock in relation with exceptionally warm waters. The equilibrium yield curve derived from the CPUE line against effort suggests that the stock is at present moderately exploited, the present catches being some 20 percent below the maximum potential estimated by pooling together the various fishery sections (Fig. 19). On the other hand, if the catchability coefficient is strongly negatively related to population size, the maximum potential yield may have been exceeded, and the population may be overfished.

Interaction between fishery segments

Processing catch and CPUE data by combining the various segments of the white seabass fishery may lead to at least partly erroneous conclusions since the segments exploit various age groups of the stock in different proportions, and since catchability coefficients of the various segments may vary differently. The pier and jetty fishery takes juvenile "sea trout" nearshore and in estuaries. The U.S. partyboats take large numbers of juveniles but adults are also caught. The U.S. private boat catch is probably similar to a mixture of the pier and jetty and partyboat fisheries. The U.S. commercial fishery operating in both California and Mexican waters fishes with large mesh gill nets (6-inch mesh or larger). Although age 4 white

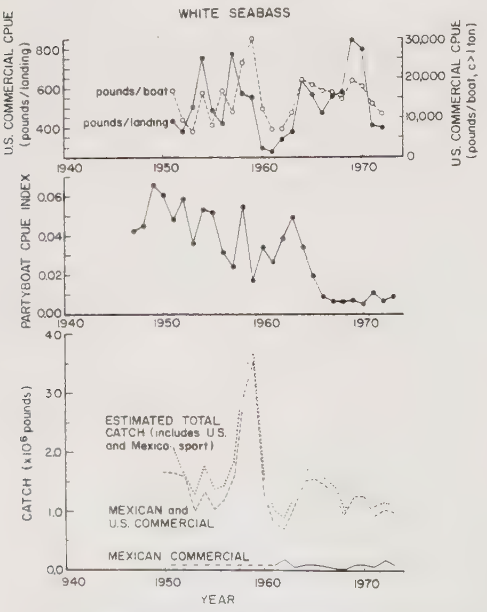

Figure 18.—Catches and CPUE for the various segments of the white seabass fishery.

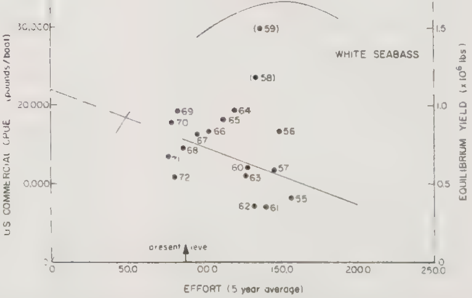

Figure 19.—Relationship between commercial CPUE and effort and the corresponding estimates of surplus production for white seabass.

Table 21.—White seabass age composition of catches in 1973 for three fishing segments.

Age	U.S. commercial	U.S. partyboat	Pier & jetty	Total
		No. of Fish		
1	0	236	773	1.009
2	0	2,361	7.727	10.088
3	0	708		708
4	223	708		931
5	1,087	1,108		2,195
6	1,546	236		1 782
7	3.095	—		3.095
8	4 180	236		4.416
9	4,333	472		4,805
10	6 966	472		7 438
11	5 030	472		5,502
12	1,703			1.703

seabass are caught by gill netters, full recruitment appears not to occur until age 9 or 10 (Table 21). The age composition of the U.S. commercial fishery may be changing since the Mexican component is declining due to a reduction in permits issued by the Mexican Government.

There has been a minimum size of 28 inches for the sport fishery; however, the bag limit has included one undersized fish per person except from 1971 to mid-1973. Due to the low catch rate, this one undersized fish essentially eliminates the minimum size requirement. Also the "sea trout" fishermen often fail to recognize their catch as white seabass and consequently, frequently violate the minimum size regulation.

In order to take into account these differences and to detect the possible interactions between various fishery segments, a yield per recruit analysis was conducted using the computer program MGEAR (Lenarz et al., 1974). This program simultaneously calculates Y/R values for a multiple gear fishery as in the case of the white seabass. The following three fisheries were included: U.S. commercial gill nets, U.S. partyboats, and U.S. pier and jetty. The U.S. private boat and both Mexican fisheries were not included because of the unavailability of catch and age composition data. Therefore, it is implicit that they are a component of natural mortality. If they fluctuate they can affect the results of the analysis.

The necessary growth and mortality parameters were taken from Thomas (1968). His estimates for instantaneous mortality coefficients were reexamined and a new value of 0.13 was estimated for *M*, based on a regression of total mortality rates for 1958, 1959, and 1960 (obtained by cohort analysis) and for 1973 (obtained by catch curve analysis) upon effort measured in number of boats with an annual catch in excess of 1 ton. Thomas gave a value of $M = 0.303$. For 1973, *Z* was estimated to be 0.50 from age composition data for the U.S. gill net fishery provided by Rob Collins, CDFG. These data were also analyzed to generate values of fishing mortality for the various age groups and gear types (Table 22). This was done by dividing total *F* among the fisheries according to the proportion of total catch of each fishery.

Since the estimates of *M* are 0.13 and 0.30, the Y/R analysis was performed for $M = 0.13$, 0.20, and 0.30. It was also assumed that all undersized fish caught are released and do not subsequently die. Size limits or alternative fishing intensities may influence future recruitment; unfortunately the analysis could not take this into account.

Results of the analysis indicate that if a uniform minimum size limit was set such that Y/R for the entire fishery would be maximal, a 12 percent gain in Y/R would be realized ($M = 0.13$, minimum size = 96 cm). The expected increase would be only 4 percent if $M = 0.20$ (minimum size = 71 cm), and no gain would be expected if $M = 0.30$, whereupon no size limit should be imposed. These changes in yields are independent of the 20 percent gain in yield to be expected from increased effort described above.

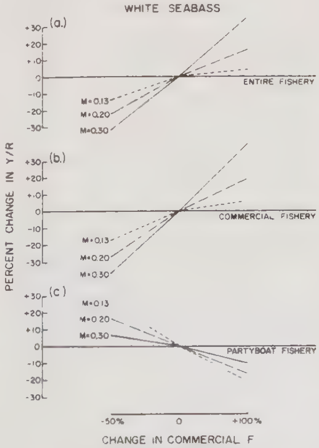

Figure 20.—Changes in Y/R for white seabass if only *F* for commercial fishery is changed.

Table 22.—Estimates of *F* for three segments of the white seabass fishery, for $M = 0.13$, 0.20, and 0.30.

Age	U.S. commercial	U.S. partyboat	Pier & jetty
$M = 0.13$			
1	0	0.0018	0.0061
2	0	0.0221	0.0724
3	0	0.0123	0
4	0.0029	0.0123	0
5	0.0164	0.0123	0
6	0.0274	0.0123	0
7	0.0656	0.0123	0
8	0.1105	0.0123	0
9	0.1501	0.0123	0
10	0.3591	0.0123	0
11	0.4566	0.0123	0
12	0.2600	0.0123	0
13-20	0.3577	0.0123	0
$M = 0.20$			
1	0	0.0009	0.0031
2	0	0.0121	0.0398
3	0	0.0090	0
4	0.0018	0.0090	0
5	0.0107	0.0090	0
6	0.0191	0.0090	0
7	0.0483	0.0090	0
8	0.0852	0.0090	0
9	0.1206	0.0090	0
10	0.2943	0.0090	0
11	0.3703	0.0090	0
12	0.2100	0.0090	0
13-20	0.2910	0.0090	0
$M = 0.30$			
1	0	0.0003	0.0041
2	0	0.0050	0.0149
3	0	0.0050	0
4	0.0008	0.0050	0
5	0.0052	0.0050	0
6	0.0152	0.0050	0
7	0.0281	0.0050	0
8	0.0534	0.0050	0
9	0.0803	0.0050	0
10	0.2020	0.0050	0
11	0.2294	0.0050	0
12	0.1420	0.0050	0
13-20	0.1950	0.0050	0

Next we examined what might happen to the Y/R for the various fisheries if the commercial fishery were to experience a 50 percent reduction in its fishing intensity or a 100 percent increase. The conclusions are:

1) A 50 percent reduction should benefit the partyboat fishery by increasing Y/R in numbers and weight. This increase is due to more large fish being available. The magnitude of the benefit decreases if the value of *M* is larger. The commercial fishery would obviously experience a decrease in Y/R. The opposite is true for each fishery for the 100 percent increase (Fig. 20a, b).

2) The trends for all three fisheries combined were similar to those of the commercial fisheries (Fig. 20a).

3) The curves in Figure 21 were essentially unaltered if the fishing intensity for the pier and jetty fishery were actually twice the original value.

4) Since the pier and jetty fishery was assumed to harvest only age 1 and 2 fish, its Y/R was unchanged by the variations in the commercial fishery.

Second, we examined what might happen if the commercial fisheries not only experienced a change in fishing intensity but also if a strict 28-inch minimum size were to be imposed on the three fisheries equally. The conclusions were:

1) A 50 percent reduction in commercial fishing plus a 28-inch size limit should benefit the sport fishery if natural mortality were less than 0.20. If, on the other hand, the commercial fishery remains unchanged or increases 100 percent, Y/R for the partyboats should be reduced because of the elimination of young age groups from the catch due to enforcement of the size limit. The larger *M* is, the greater this reduction in Y/R (Fig. 21c).

2) The size limit should improve commercial Y/R at all levels of fishing intensity except at the higher levels of *M* near 0.30. The improvement increases with lower *M* (Fig. 21b).

3) Trends in the fishery as a whole are similar to those for the commercial fishery.

4) The pier and jetty fishery would be eliminated if the size limit is enforced.

5) If the pier and jetty fishery were actually double the estimated size, a 28-inch size limit should cause the Y/R for all fisheries to increase by 5-10 percent if $M = 0.13$, by 2-5 percent if $M = 0.20$, and by 0-2 percent if $M = 0.30$ (Fig. 21).

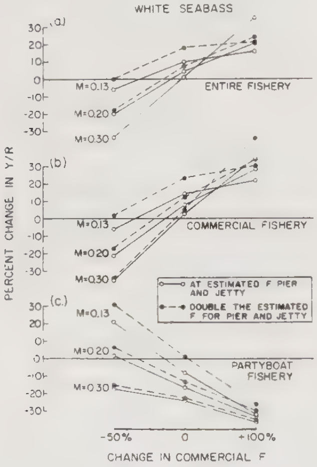

Figure 21.—Changes in Y/R for white seabass if *F* for commercial fishery is changed and at the same time a 28-inch size limit is enforced.

YELLOWTAIL

The yellowtail, *Seriola dorsalis*, is probably the most important single species to the southern California partyboat fishery, both in economics and angler preference. A large commercial fishery for yellowtail has existed in the past, and could be expanded at any time both off U.S. and Mexican shores. Therefore, it is essential to determine the present status of exploitation, maximum sustainable levels of yield, and probable interactions with the sport fishery.

Data

Data on yellowtail fisheries suffer the same shortcomings as do other primarily recreational species. Long time series catch records are available for California commercial landings in weight and for the California partyboat catch in numbers of fish. Mexican commercial landings in weight are known since 1966. The only length distributions available allowing transformation of catches in numbers to catches in weight refer to partyboat catches in 1973 and to individual samples occasionally taken from various U.S. catches (sport, commercial, and research) during the period 1952-54. Since size composition of catches is known to vary between fishery segments (see Fig. 22) and with time in relation to changes in the amount of fishing, these two sets of data are notably insufficient to build up the sport fishery catch (in weight) during the whole period considered.

Despite these limitations, annual catches by fleets have been tentatively reconstructed for two periods—1947-54 and 1966-72 respectively—selected for the following reasons: 1) Availability of length frequency distributions (and length/weight relationship); and 2) The relative stability of the amount of fishing taken as a whole during each of these two periods.

For such conditions of fishing stability, the sport fish catches were converted to weight by applying the corresponding average weight of fish in the size composition samples to all years within the respective time series.

For the various fishery segments for which no data are available—essentially U.S. sport fishery other than partyboats—estimates were made from information on their relative importance in certain years and from likely trends in their development. The importance of these estimated catches appears to be rather small compared to that of documented sections (about 1 percent of estimated total catches for the period 1948-53 and between 15 and 36 percent for the 1966-73 period). The assumptions made, though probably inaccurate in details, should provide a fair picture of actual trends (Table 23).

Annual catch per angler for the Coronado Islands (Mexico) area (CDFG statistical block 916) was chosen as the best available index of abundance. The Coronado Islands are the closest well-sampled area to the center of the yellowtail population and tend to be the mainstay of local yellowtail sportfishing in southern California, which exploits the fringe of a population which is centered off southern Baja California. Partyboat effort for pre-1960 years was calculated using the conversion 1.0073 angler/angler day based on the mean of 1960 and 1961 observations. Partyboat catch, in number of fish caught, was transformed to weight caught using the average weights of fish caught for the two periods (10.86 pounds for 1947-54 and 12.78 pounds for 1966-73). Overall standard effort was estimated by dividing total catch in weight for all fisheries by the Coronado Islands CPUE thus obtained.

Indices of apparent abundance derived from aerial surveys have also been published, but because yellowtail are seldom observed from planes, the method probably does not provide a reliable index of relative abundance for such species (Squire, 1972). Therefore, this source of data was not used in the present analysis.

Historical trends

During the warm water years of 1957 through 1959, yellowtail appeared in unusual abundance in southern California waters and angler success reached record levels. The warm water phenomena aroused interest in the effects of ocean temperature on fish distribution and availability, and Radovich (1963) presented a hypothesis that warm oceanic conditions may bring about a northward shift of the yellowtail population, and as southern California is normally at the extreme edge of the population, this movement considerably increases the local abundance. Examination of data from more recent years supports the hypothesis (Radovich, 1975) and a scatter diagram of CPUE in numbers per angler day at the Coronado Islands versus annual mean sea surface temperature at Scripps Pier in La Jolla shows a distinct relationship (Fig. 23). On the other hand, the temperature relationship is not as pronounced for the common range of water temperatures. It is still worthwhile to examine the effects of fishing in more "normal" years.

The period 1948-54 corresponds to the end of a stable era of high exploitation by U.S. commercial boats operating mainly near Magdalena Bay, Baja California. During this period, initiated in 1935, commercial landings fluctuated between 4 and 10 million pounds with an average of 6.3 million pounds. Between 1948 and 1954, U.S. commercial landings and sport catches amounted to about 92 percent and 8 percent of total catches respectively.

Cannery demand for yellowtail ceased after 1954, causing a considerable drop in U.S. commercial yellowtail fishing operations. As a consequence, their landings have fluctuated around 230,000 pounds since 1955. Since then a commercial fishery has developed in Mexico, and sport catches from California and Mexican boats have more than doubled. Yet these overall landings remain far below the previous level. During the 1966-72 period total catches have averaged 71 percent below the 1947-54 level. Simultaneously the catch per angler (partyboat) increased by about two-thirds above the 1948-54 level and the overall effort is now at 10 percent of its level at the end of the period of intensive fishery (1948-50) (Table 24). The result of such changes in participation in this fishery is well illustrated by the following percentages (of total catches):

Period	U.S. commercial	Mexico commercial	Sport fisheries
1948/54	95%	Negligible	5%
1966/72	11%	37%	52%

Reported mean weights of fish caught (about 10 pounds in 1935 according to Fry (1973), 10.86 pounds in 1952-54, and 12.78 pounds in 1973) are in agreement with the general reduction in the amount of fishing deduced from trends in total

Table 23.—Yellowtail: estimated annual catches.

Year	U.S. commercial		Mexico commercial (10^3 lb)	U.S. partyboat (10^3 fish)	Other sport combined (U.S. + Mex.) estimate[1] (10^3 fish)	Total sport catch (10^3 fish)	Total[3] sport catch (10^3 lb)	Estimated total catch (10^3 lb)
	California (10^3 lb)	Mexico (10^3 lb)						
1947	103.7	9,849.1		6.95	(1.6)	(8.6)	(93.4)	(10,046)
1948	246.6	10,138.1		13 03	(4.7)	(17.7)	(192.2)	(10,577)
1949	15.9	7,301.8		17.71	(3.7)	(21.4)	(232.4)	(7,550)
1950	5.7	3,524.2	assumed	6 97	(1.5)	(8.5)	(92.3)	(3,622)
1951	14.5	4,655.3	to be	23.72	(4.8)	(28.5)	(309.5)	(4 979)
1952	51.1	9,395 9	negligible	59.26	(12.2)	(71 5)	(776.5)	(10,224)
1953	14.4	5,198.0		27 70	(5.8)	(33.5)	(363.8)	(5,577)
1954	11.8	1,644.9		40.87	(9.1)	(50.0)	(543.0)	(2,200)
1955	5.6	158.8	—	36.47	(8.0)	(44 5)	—	—
1956	18.6	352.3	—	29.20	(6.8)	(36.0)	—	—
1957	150.9	358.1	—	242.69	(56.8)	(299.5)	—	—
1958	105.5	64.1	—	123.38	(29.6)	(153.0)	—	—
1959	207.2	24.1	—	457.35	(112.1)	(569.5)	—	—
1960	156.5	92.1	—	254 97	(63.5)	(318.5)	—	—
1961	80.7	300.1	—	42.12	(10.8)	(52.9)	—	—
1962	37.1	151.4	611.1	21.79	(5.7)	(27.5)	—	—
1963	25.4	44.3	261.3	41.68	(11.3)	(56.6)	—	—
1964	25.9	84.2	1,481.4	38.00	(11.5)	(49.5)	—	—
1965	12.5	115.3	938.3	11.68	(11.3)	(23.0)	—	—
1966	35.9	209.3	761.6	72.94	(29.0)	(102.0)	(1,303.6)	(2,310)
1967	13.2	137 5	642.7	16.00	(24.0)	(40.0)	(511.2)	(1,305)
1968	22.5	140.7	1,901.1	35.01	(39.4)	(74.5)	(952.1)	(3,016)
1969	11.7	222.4	671.2	44.70	(57.3)	102.0)	(1,303.6)	(2,209)
1970	56.3	127.9	528.0	72.55	(53.4)	126.0)	(1,610.3)	(2,323)
1971	31.0	359 5	30.8	17.30	(40.7)	(58.0)	(741.2)	(1,163)
1972	96.1	163.0	[2](740.0)	31.08	(46.0)	(77.0)	(984.1)	(1,983)
1973	82.5	152.8	1,869.2	189 89	(100.1)	(290.0)	(3,607.2)	(5,712)

[1] Mean between maximum and minimum guesses, calculated as following: (a) Ratio Mexican partyboat catch to U.S. partyboat catch: max = 0.23 (1961), min = 0.03 (1971); (b) Ratio U.S. private boat catch to U.S. partyboat catch: constant = 0.13 (1964), increasing = 0.01/(year-1950); (c) Long range partyboat catch as reported.

[2] Preliminary estimate based on 550,000 lb caught in 9 months and average catch/quarter from 1966 to 1971, other Mexican data courtesy of Instituto Nacional de Pesca.

[3] Based on mean weights of samples taken from partyboats ($\bar{w}$ = 12.78 lb) in 1973 and from sport, commercial, and research boats. ($\bar{w}$ = 10.86 lb) in 1952-54.

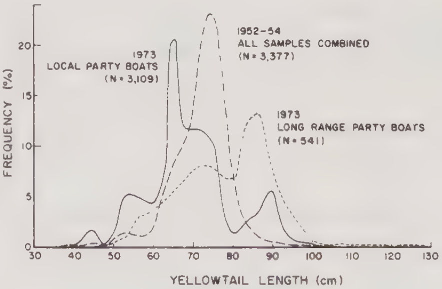

Figure 22.—Yellowtail length frequency distributions for 1952-54 and 1973.

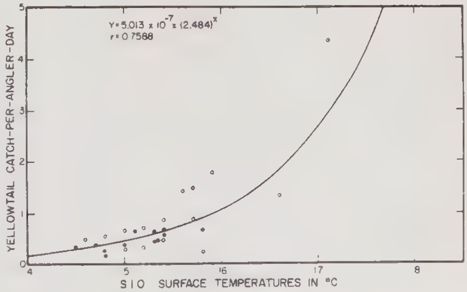

Figure 23.—Yellowtail CPUE in number per angler at the Coronado Islands plotted against annual mean sea surface temperature at Scripps pier (from Radovich, 1975); solid points are years used in production model.

catch. Length composition shows an increase in the proportion of older fish between 1952-54 and 1973.

Present state of exploitation

Using Gulland's (1969) approximation method for assessing equilibrium curve, yellowtail CPUE data (Table 24) for partyboat anglers were plotted against average total effort (average of past 3 years in order to take into account the approximately 6 years duration of exploited phase). Since data are only available for the periods of 1948-54 and 1966-72, respectively, the number of points is small; however, they appear to give a fair picture of the above trend in recent history of the fishery. A slightly curved line describes the relationship between CPUE and total effort (Fig. 24), and the derived equilibrium yield curve shows a maximum of about 8.5 million pounds for a corresponding total effort of 2.5 to 3 × 10^6 Coronado Islands partyboat angler standard units, i.e., roughly 8 to 10 times the 1966-72 level. Estimated MSY is slightly above the average catch for the 1935-54 period of high fishing.

Under the present conditions of exploitation, determination of the exact positions of the potential and of the corresponding effort is not essential. Although the data used suffer from various limitations, it seems reasonable to conclude that stock abundance increased following the reduction in the amount of fishing since 1955. The stock appears to be in very good health. Sport catches have improved under the present level since exploitation has been far from maximum sustainable levels. The stock is capable of producing much higher yields (3-4 times or more), however, at the cost of a corresponding decrease in sport CPUE (Fig. 24). It should also be noted that neither the southward extension of the stock nor its relationship with other stocks located in the Gulf of California and more southern waters, is very well known. It is, at present, assumed that such stocks do not contribute substantially to the California fisheries. If this assumption is not to be confirmed, expansion of fishing in more southern waters might provide higher yields.

Table 24.—Yellowtail: CPUE and estimated total effort.

Year	Partyboat CPUE		Estimated total effort 1,000 standard units[1]
	Coronado Islands fish/angler	Estimated lb/angler	
1947	0.229	2.490	4035
1948	0.232	2.521	4197
1949	0 290	3.146	2400
1950	0.174	1.891	1914
1951	0.451	4 903	1016
1952	0.620	6.734	1518
1953	0.364	3.948	1413
1954	0.664	7.211	305
1955	0.644	—	—
1956	0 489	—	—
1957	1 913	—	—
1958	1.315	—	—
1959	4 312	—	—
1960	1.418	—	—
1961	0.559	—	—
1962	0.518	—	—
1963	0.869	—	—
1964	0.716	—	—
1965	0 304	—	—
1966	0.886	11 325	204
1967	0.380	4 860	268
1968	0.662	8.460	357
1969	0 452	5.779	382
1970	0 633	8 092	287
1971	0.319	4 082	285
1972	0.455	5 802	309
1973	1.441	18.414	315

[1] Standard effort unit is Coronado Island angler day Total effort is the hypothetical amount of standard effort units necessary to take the entire catch

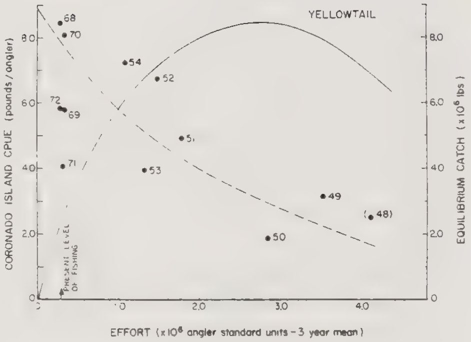

Figure 24.—Relationship between Coronado Islands CPUE and effort and the corresponding estimates of surplus production for yellowtail.

Analysis, discussion of present management measures

Between May and August the U.S. commercial yellowtail fishery is now subject to several limitations: Catches per trip are limited to 500 pounds per fisherman and 2,500 pounds per boat; use of purse seine and round haul nets is prohibited, and gill nets must have a minimum mesh size of 3.5 inches. Similarly, a daily bag limit of 10 fish is applied to the sport fishery which uses only hook and line. Considering the present low level of exploitation of the stock and the fact that 50-60 percent of the total catches are taken in unregulated waters off Baja California, such regulations are not justified on biological grounds.

In addition, a 28-inch size limit has been introduced for the California commercial fishery. Apparently such a measure has been based on size of first maturity (all fish are said to be mature as 3 years old, or 27.8 inches). However, there is no scientific evidence, either in yield per recruit or in recruitment/parental stock to justify such regulation. Although *M* is not known, the present low level of exploitation strongly suggests that the maximum yield per recruit would be achieved for a smaller size at first capture than the legal one which represents about 0.55 the maximum sizes of fish caught. Examination of yield per recruit tables (Beverton and Holt, 1966) indicate that if $M/K = 1.50$ ($K = 0.136$), and fishing mortality is low (less than ⅓ M), yield per recruit could potentially be increased from 6 to 16 percent by lowering minimum size from 28 inches. If $M/K = 0.75$ only a 1-4 percent increase would be expected, as 28 inches is nearer proper minimum size for low mortality rates. Stock recruitment relationship should not raise particular problems at the present level of fishing, and even for substantially higher ones, since the long life span of yellowtail and the subsequent high number of year classes present in the population should make it less vulnerable to successive low recruitments. It should also be mentioned here that the minimum mesh size does not appear to correspond to the legal minimum size and sublegal size fish may be captured. Such a situation is inappropriate both on biological and economic grounds.

It can be concluded that at present no limitation appears to be necessary in the yellowtail fishery. However, the limited potential of the stock would require early formulation and implementation of proper management measures, should the fishery expand in the future.

INTERACTIONS

Fisheries seldom act in the absence of important interactions from other fisheries, species composition and trophic relationships, and exogenous environmental influences. These interactions are complex in southern California waters. Here we have selected some relevant aspects for quick investigation. Fisheries interactions are an important aspect of the northern anchovy exploitation controversy, and are briefly discussed, with emphasis on the live bait anchovy supply. Species composition of both commercial wetfish fleet and partyboat catches have undergone large changes in recent years. A strong argument against large-scale exploitation of the northern anchovy has been based on the necessity of this species as forage for game fish. Discussion of these topics may be of use in gaining perspective on the status of the individual stocks discussed in this report.

Northern anchovy fisheries interaction and allocation

Three separate fleets presently exploit the northern anchovy, *Engraulis mordax*: The southern California live bait fleet; the southern California wetfish fleet; and the Mexican wetfish fleet based in Ensenada (Table 25). To these may be added the possibility of the entry of Russian vessels as evidenced by recent experimental offshore trawling for northern anchovy. These fisheries must be expected to show both short- and long-term interactions, and the nature of these interactions should be a major input to plans for allocation of the anchovy resource to the various users.

Table 25.—Anchovy fisheries.

Exploiter	Geographic area of exploitation	Age of recruitment	Present catch (10^3 tons)	Present catch value ($\$10^3$)	Ex-vessel price index $/ton	Probable catch in 5-10 yr (10^3 tons)	Regulating agency
Southern California wetfish fleet (reduction)	Inshore, near San Pedro and Port Hueneme facilities (San Diego in future)	2	100	[1]5,000	30-50	100-200	Calif. Fish. Game Comm.
Southern California live bait fleet	Shallow inshore near sportfishing ports in southern California	1	10	[2]direct 5,000 [3]indirect 5 000 – Total 10,000 –	[5]660 +	10-15	Calif legislature
Mexican wetfish fleet (reduction)	Inshore near Ensenada	1-2	30	[4]1,000 +	[6]25-35 +	50-200	Mexico (U.S. Gov't. has authority for negotiation)
USSR High seas trawler/factory ships (canning)	Offshore	3	0	0	0	0-100	USSR (U.S. Gov't. may have strong control)

[1] 100,000 tons @$50/ton (price generally lower).

[2] 1,000,000 scoops @$5/scoop

[3] 600,000 partyboat angler-trips @$8/trip, assuming the partyboat industry is completely dependent on live bait. True indirect value will be less.

[4] 30,000 tons @$33/ton. Economic value to Mexico not comparable with U.S. values.

[5] Based on $5/15 pound scoop. Inclusion of indirect value would increase index.

[6] Economic worth to Mexico may be greater than U.S. dollar value suggests.

The problem of allocation has generally been avoided since simple, conservative management has been acceptable to the interested parties. Future developments may alter present attitudes toward the fishery in California, and exploitation by foreign fleets will certainly undergo expansion in the near future. Unfortunately, each fishery is presently regulated by a different agency and it will be impossible to manage the stock scientifically or efficiently unless the various agencies are able to establish a common basis for discussion and optimization of anchovy exploitation. Presently there is a healthy cooperation and communication at lower levels, as is necessary for formulation of management alternatives. Cooperation, however, must occur at the highest levels of State, Federal, and foreign governments so that coordinated and responsive management is implemented. Establishment of such a forum will be difficult.

An initial attempt at establishing suitable criteria for allocation might be based on price paid per ton of fish (Table 25), which tends to reflect the value consumers put on the fishery product. Such an index could be improved by including other factors such as yield relative to maximum (or optimum) sustainable yield and variations in price with supply, or these factors could be included as components in a general allocation model. By this simple price index, the live bait fishery far outweighs the reduction fishery in importance and should be given full consideration.

Live bait anchovy fishery

The southern California live bait fishery is the supplier of bait for sport fishermen. The bulk of the bait goes to partyboat utilization. Thus, the live bait fishery operates under two simultaneous sets of constraints. Supply is limited by availability (CPUE) of anchovies, while demand is determined by sport fishing activity. Fortunately, analysis of these relationships is possible due to the availability of voluntary live bait catch and effort logbook data and extensive partyboat effort data collected by CDFG.

Supply was approached as a problem in CPUE, with catch measured in scoops (about 15 pounds of fish) and effort in boat trips. The CDFG Statistical regions 6, 7, and 8, corresponding to Santa Barbara, Los Angeles, and San Diego areas respectively, were investigated separately.

Annual CPUE values were calculated as annual catch divided by annual trips. This glosses over seasonal variation, but gives a good view of the long-term trend (Fig. 25). Assuming fishing vessels have not changed in fishing power, and neglecting sardine catches, there has been a large increase in availability of anchovies in recent years.

Table 26.—Anchovy bait fishery—long and short term effects of reduction fishing.

Years	Region 6 (Santa Barbara)			Region 7 (Los Angeles)			Region 8 (San Diego)		
	Winter[1]	Summer[2]	ln (s/w)	Winter[1]	Summer[2]	ln (s/w)	Winter[1]	Summer[2]	ln (s/w)
Nonreduction									
60-61	—	157.6		186.4	462.1	0.908	319.5	791.6	0.907
61-62	151.0	265.8	0.565	286.9	407.7	0.351	708.3	518.7	−0.312
62-63	142.8	195.9	0.316	241.3	351.5	0.378	478.0	571.8	0.179
63-64	117.5	202.4	0.544	192.9	454.4	0.857	203.9	640.1	1.144
64-65	138.1	191.7	0.328	232.0	425.3	0.606	243.6	546.4	0.808
67-68	250.5	141.4	−0.572	940.8	574.8	−0.493	368.1	581.0	0.456
$\bar{x}$	160.0	192.5	0.236	346.7	446.0	0.434	386.9	608.3	0.531
σ	52.09	43.15	0.467	293.3	74.49	0.510	184.7	98.53	0.535
Reduction									
65-66	220.8	243.6	0.098	296.1	477.9	0.479	287.8	603.5	0.740
66-67	138.0	229.6	0.509	334.1	513.6	0.430	349.7	1,303.8	1.316
68-69	225.8	294.8	0.267	465.1	728.4	0.449	469.4	699.0	0.398
69-70	141.5	163.8	0.146	319.8	773.9	0.884	547.0	887.4	0.484
70-71	69.8	133.5	0.648	514.0	526.3	0.024	673.4	930.2	0.323
71-72	83.8	177.0	0.748	717.3	854.1	0.175	784.3	2,031.1	0.952
$\bar{x}$	146.6	207.1	0.403	441.1	647.7	0.407	518.6	1,075.8	0.702
σ	65.91	59.5	0.271	160.9	159.1	0.295	189.5	526.6	0.381

[1] $\Sigma c/\Sigma f$ for November, December, January, and March

[2] $\Sigma c/\Sigma f$ for June, July, and August

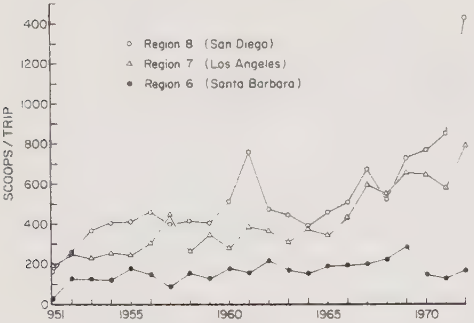

Figure 25.—Anchovy live bait CPUE (annual scoops/trip).

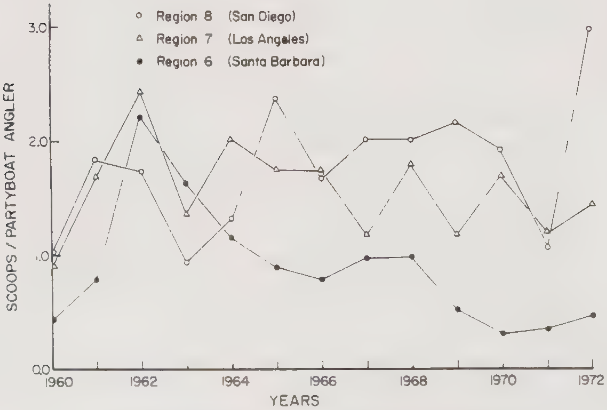

Figure 26.—Anchovy live bait catch per partyboat angler (scoops/angler).

Both the San Diego and Los Angeles regions show this trend. The Santa Barbara region appears to have experienced an increase in availability up to 1969, but it suffered a severe decline in CPUE in 1970, 1971, and 1972.

Separation of short-term (seasonal) and long-term trends in availability, vis-a-vis the reduction fishery, was accomplished by separating CPUE observations into long-term groups (reduction fishing seasons of 1965, 1966, 1968, 1969, 1970, and 1971, and nonreduction seasons of 1960, 1961, 1962, 1963, 1974, and 1967), and into short-term groups (reduction period, winter—November, December, January, and March; non-reduction period, summer—June, July, and August). The long-term availability has likely increased since the mean CPUE's for all three geographical regions for the summer period were higher for the reduction years than for the previous non-reduction years (Table 26). Winter availability shows a similar trend for Los Angeles and San Diego, but a slight decrease for Santa Barbara, particularly for the most recent years. The tendency for increased availability in recent years, despite the reduction fishery, presumably has been a result of an increase in anchovy abundance (we have assumed an increase in vulnerability or fishing power has not occured). Values of anchovy bait CPUE (Fig. 25) show a weak correlation with egg-and-larvae indices of abundance of the central stock of anchovies (r San Diego = 0.65, r Los Angeles = 0.51, r Santa Barbara = 0.45). Offsetting the years to account for the younger age of bait anchovies did not give significant increases in correlation coefficients.

Short-term changes in anchovy bait availability, presumably caused by decrease in winter availability due to reduction fishing, were examined by comparing summer/winter ratios (in natural logarithms) of CPUE during years of reduction fishing with ratios for years in which there was no reduction fishery (Table 26). Mean relative winter availability decreased 12 percent in the Santa Barbara region and 12 percent in the San Diego region during years of reduction fishing, but in the Los Angeles region, in which reduction fishing was presumably the heaviest, the mean of ratios showed an 8.6 percent increase in relative winter availability. The variance of the log ratios is large so no tests of significance were attempted.

It is concluded that bait anchovy availability has not shown either long- or short-term decreases connected with the anchovy reduction fishery up to the 1971-72 level of reduction catch. The San Diego and Los Angeles bait regions appear healthy, but the Santa Barbara region shows a large anomaly starting in 1970.

The live bait fishery is also highly influenced by bait demand, with commitments to bait users varying with amount of sport fishing effort. Letting the number of partyboat anglers be an index of demand (as we have no values for private boat utilization of bait) and letting the bait catch indicate the supply for that market, an index of bait supply to the sport fishermen can be calculated. The trend of live bait catch per partyboat angler shows a fluctuating, but fairly constant, supply to the angler for the San Diego and Los Angeles regions, but the Santa Barbara region shows a long downward trend since 1962 (Fig. 26). The years 1969 through 1972 show extremely poor bait supplies in Santa Barbara and the 1969 point is unusual in that CPUE was the highest on record for the Santa Barbara area (Fig. 25). Examination of trends in effort show the expected reduction in effort for San Diego and Los Angeles areas where CPUE increased, but shows a decrease in effort for Santa Barbara when CPUE also decreased (Fig. 27). This suggests that either commitments to the fishermen decreased, or it became economically unfeasible to fish at the low level of bait availability, which is unlikely as the price of bait can be adjusted accordingly. The anomalous behavior of the Santa Barbara fishery in 1969 supports the former hypothesis.

The ratio of bait catch to partyboat anglers was suggested as a measure of commitment above. Letting K be a constant value of commitment in scoops per partyboat angler, a linear relationship between the ratio of bait effort (f_b) to anglers (f_s) and the reciprocal of bait CPUE can be described.

Letting C_b be bait catch,

$$\frac{C_b}{f_s} = K.$$

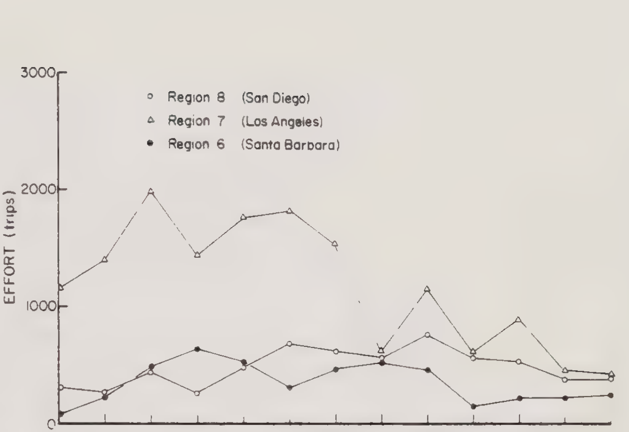

Figure 27.—Anchovy live bait effort (trips).

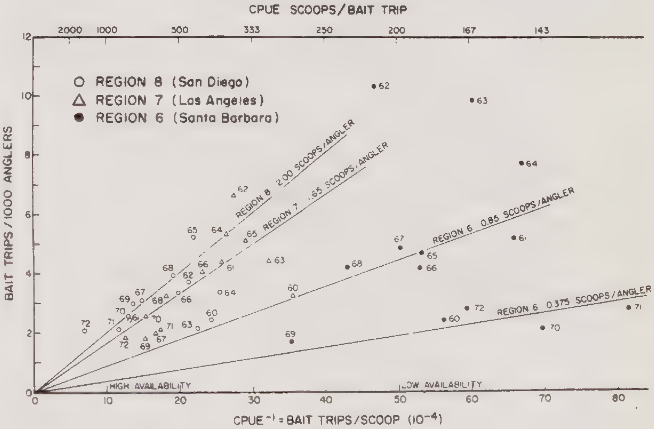

Figure 28.—Anchovy live bait demand commitment and supply.

$$\frac{C_b}{f_s} \times \frac{f_b}{f_b} = \frac{f_b}{f_s} \times \frac{C_b}{f_b} = \frac{f_b}{f_s} \times \text{CPUE} = K.$$

$$\text{or } \frac{f_b}{f_s} = K\ \text{CPUE}^{-1}.$$

A plot of f_b/f_s vs CPUE^{-1} (Fig. 28) shows a good linear relationship for Los Angeles and a fair one for San Diego. The early years 1960 and 1963 appear as outliers in both plots. San Diego (K = 2.0 scoops/angler) shows a somewhat higher commitment than does Los Angeles (K = 1.65 scoops/angler). Santa Barbara is again anomalous in not showing any well-defined relationship. Possible relationships are K = 0.85 scoops/angler for 1969-72, again suggesting a reduction in level of commitment for recent years.

Levels of commitment can presumably change due to changes in the relative number of nonpartyboat anglers buying live bait, or due to changes in sport fishing methods and target species. For example, fishing for rockfish requires less bait per angler than fishing for game fish where large amounts of chum are used. This partly explains the lower levels of commitment in the Santa Barbara area where bottom fishing predominates. It must be concluded that

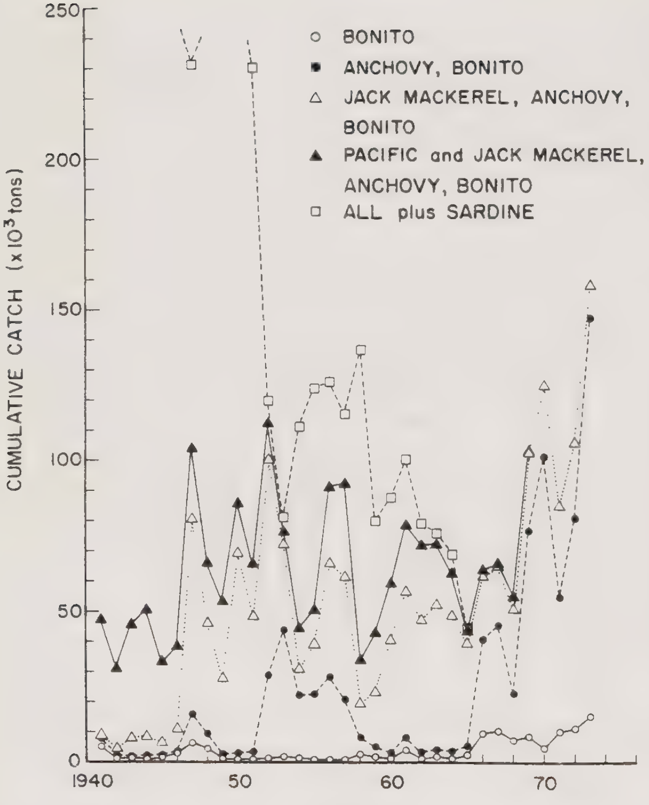

Figure 29.—Total commercial catch of fish species exploited by purse seine wetfish fleet, 1941-73.

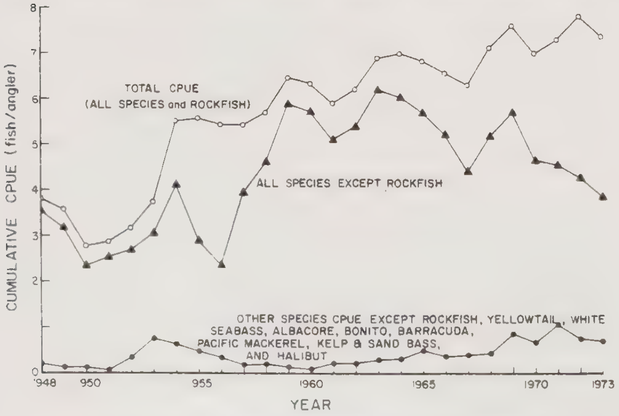

Figure 30.—Total partyboat CPUE (fish/angler) for southern California.

low availability in the Santa Barbara area is a condition which has existed at least since 1951, and is probably not the result of the anchovy reduction fishery. Moreover, there is some evidence that the Santa Barbara bait fishery has established lower commitments rather than increasing effort to maintain the supply to the sport fisheries. Lack of further information on the Santa Barbara bait fleet and fishery prevents a definite conclusion, and there may be other factors which explain this anomalous behavior.

Southern California wetfish fishery

Species caught by the wetfish fleet include Pacific sardines, Pacific mackerel, jack mackerel, Pacific bonito, and northern anchovy, and small amounts of a variety of other species. The majority of the commercial catch is landed in the Santa Barbara, Los Angeles, and San Diego regions with the San Pedro wetfish fleet accounting for most of the fishing effort. Prior to the collapse of the sardine stock, almost the entire effort was directed toward sardines. Since the 1951 collapse, the catches of the four other species have sustained the fishery but have fluctuated for various reasons (Fig. 29). Documentation of the fishery interactions between wetfish species is useful in the assessment of any one of the stocks.

After the virtual collapse of sardines in 1951 and until 1963, the total catch of the five species varied between 80,000 and 130,000 tons annually. When sardine catches temporarily improved, catches of the others usually dropped. The anchovy was canned for human consumption and made up from one-quarter to one-third of the fishery until 1958. Jack mackerel catches sustained the fishery when sardines were low and after the demand for canned anchovies declined. Pacific mackerel catches were consistent from 1954 until the collapse of the stock in the mid-1960's. Bonito catches were low because of low stock sizes in the early 1950's and lack of processors' demand. The combined catch of all five species reached a low of 43,000 tons in 1965.

Beginning in 1966 the composition of the wetfish catch changed. Sardine and Pacific mackerel catches failed to recover and fishing moritoria were imposed in 1967 and 1971 for the two stocks respectively. Bonito catches jumped in 1966 and have since fluctuated depending somewhat on processor demand (Perrin and Noetzel, 1970). The jack mackerel catch has dropped apparently as the result of effort being redirected toward anchovies. This new interest in anchovies is due to the California Fish and Game Commission allowing anchovy reduction for fish meal in the fall of 1965. Recent high catches are a result of high prices paid for fish meal brought on by the collapse of the Peruvian anchoveta fishery.

Southern California partyboat fishery

The status of the partyboat fishery is largely the result of the satisfaction obtained from the angling experience; however, angler satisfaction is a difficult concept with which to work. It is generally not quantifiable as is profit in the case of commercial fisheries. It varies widely between anglers, and generalizations are likely to result in overlooking the variety of individual experience. In view of these problems, the following discussion attempts to assess the status of the partyboat fishery in simple terms with enough quantifications to allow rough comparisons between years.

The partyboat catch is composed of a multitude of species of varying interest to the angler. Total CPUE regardless of species, in number of fish per angler-trip, shows an upward trend since 1950, having doubled the overall catch rate since that time (Fig. 30). Such a trend in CPUE of combined species has a limited meaning in assessing angler satisfaction, however, as species composition of the catch is of prime importance to the sport fisherman.

Nine species comprise the bulk of the landings (Fig. 30). These species were divided into three groups based on a subjective classification. The first group is composed of large sport fish: white seabass, yellowtail, and albacore (Fig. 31). The second group is composed of smaller sport fish: barracuda, bonito, and Pacific mackerel (Fig. 32). The third group is composed of "food" species: kelp and sandbass, rockfish and halibut (Fig. 33). The CPUE was calculated as total partyboat catch divided by total anglers, which in this case includes long-range partyboat data.

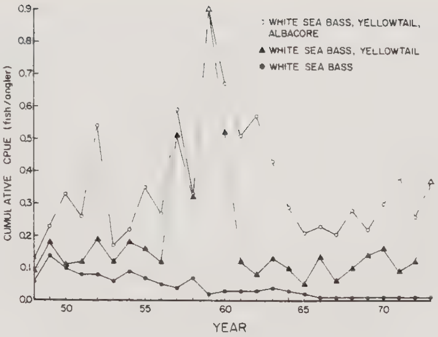

Figure 31.—Large sport fish partyboat CPUE.

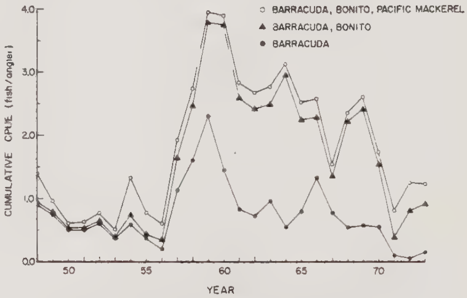

Figure 32.—Small and medium sport fish partyboat CPUE.

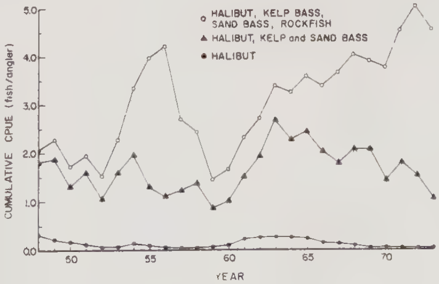

Figure 33.—"Food" fish partyboat CPUE.

Both the large and small sport fish groups show large increases in catch rate during and following the warm water years. Catch rates for these functional groups have tapered off more recently and appear to have returned to levels comparable to the early 1950's. The species composition within these groups has changed considerably since that time, however.

The biggest change that has occurred in the partyboat fishery is the increased effort directed toward the "food" group, particularly rockfish. The rockfish resource appears to have been "discovered" in the mid-1950's, but was later ignored in favor of the highly available sport fish species in the warm water years. With the slow decline of sport fish availability to previous levels, the "food" species were again sought. It appears likely that the period of high sport fish abundance caused an increase in the catch level necessary for angler satisfaction. This need for more fish has been filled mostly by rockfish, which furnishes the expected catch, but angler satisfaction falls short of that provided by the livelier sport fish. The ability of the rockfish resource to withstand increased harvesting is unknown and should be seriously investigated.

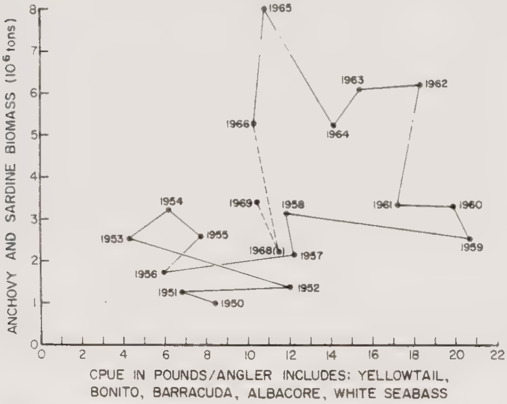

Figure 34.—Relationship between anchovy plus sardine biomass and game fish partyboat CPUE for 1950-69.

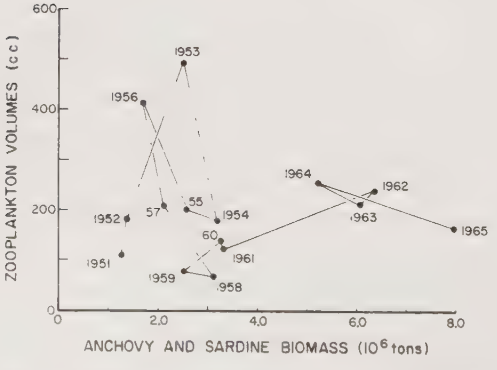

Figure 35.—CalCOFI mean zooplankton volumes and anchovy plus sardine biomass estimates for 1951-65.

In summation, the partyboat fishery experienced an increase in availability of medium and large sport fish during and following the warm water years. Catch rates for these groups of fish are now returning to levels similar to those of the early 1950's. The fishery appears to be producing an angler experience comparable to or better than that of the early 1950's and therefore must be considered to be fulfilling angler expectations no poorer than they did in the early 1950's.

Sport fish-anchovy relationships

The trophic relationships are complex between forage species such as anchovies and sardines and predatory game fish species such as yellowtail, barracuda, bonito, white seabass, and albacore. An attempt to describe the food webs and to quantify energy flows between trophic levels for the last 20 years is beyond the scope of this report. Furthermore, necessary estimates of growth rates, daily food rations, and predator biomass do not exist. On the other hand, biomass estimates for sardines and anchovies and partyboat CPUE provide enough information for a superficial examination of the relationship between biomass of these forage species and the availability of the major game fish.

A plot of anchovy and sardine biomass estimates for all stocks versus combined partyboat CPUE (pounds/angler) for yellowtail, barracuda, white seabass, bonito, and albacore for the years 1950-69 tend to support the general theory of Brocksen, Davis, and Warren (1970) (Fig. 34). They hypothesize that if forage is limiting, then a negative relationship would be expected between forage biomass and predator biomass such that high levels of predators should reduce forage to low levels, and at low levels of predators, forage would grow to high levels. If the system becomes more productive as a result of environmental events, the relationship still holds except at much higher levels of both prey and predator biomass.

The data for southern California suggest three time periods. The first is the years 1950-56 when forage biomass and game fish index were both relatively low. The second, 1957-60, appears to be a transitional period during which forage biomass remained low but the index of game fish increased greatly as a result of the warm water.

The third period, 1961-66, appears to be a regime of greater productivity in general. An examination of CalCOFI data from Thrailkill (1969) suggests a slight increase in plankton volumes for the 1960's over the 1950's if 1953 and 1956 are ignored (Fig. 35). This trend may be more significant if salps are eliminated from the volume means. If the first and third periods are treated separately, assuming levels of productivity are indeed different, it might be concluded for each that forage biomass is influenced by the abundance of these game fish.

Unfortunately this analysis is an oversimplification of the relationship and is not supported by a more detailed examination of the evidence. First of all the food web is much more complex than suggested by the analysis. The number of forage species is greater than two. Squid, for example, are also important but annual estimates of biomass are not available. The abundance of forage species in any one year may be more dependent on recruitment than on grazing by predators. Information from MacCall (1973) suggests that anchovy recruitment has been relatively constant for years 1960-65. The partyboat CPUE does not include all the major predators; birds and marine mammals must account for a large proportion of the annual mortality. Albacore has been included in the CPUE index for two reasons. First, the original CDFG partyboat statistics includes albacore trips and, second, stomach samples of albacore collected in southern California have contained 55 percent anchovies by volume (Pinkas, Oliphant, and Iverson, 1971). The species of game fish included in the CPUE index are highly migratory so that the quantity of game fish present in any one year is most likely due to contemporary conditions of the ecosystem rather than population dynamics of the game fishes. Furthermore, partyboat CPUE may not be proportional to biomass of game fish.

Additional evidence does not support the contention that increases in forage biomass will increase game fish availability in southern California nor does it support the contention that game fish influence anchovy stock as much as suggested in Figure 35. Examination of the time series in Figure 35 suggests that the increased availability of game fish during warm water years did not reduce anchovy-sardine biomass as theory would suggest. Either the productivity of forage increased simultaneously or the predator species being considered did not influence forage biomass significantly. The high CPUE values for the third period are not the result of a composite of similar increases for the five species but result mainly from increased catch of bonito which apparently established a larger population in the southern California bight during the warm water years. Whereas the CPUE declined during the mid-1960's while forage supplies increased, the abundance of game fish is not obviously dependent on forage supplies.

The biomass of anchovies and sardines lost to natural mortality each year can be estimated by $\Sigma M_i \bar{B}_i$ where instantaneous rate of natural mortality M_i is assumed to equal 1.0 and 0.8 for anchovies and sardines respectively, and where $\bar{B}_i$ is the annual average biomass of each species. The estimates average 1.0, 3.0, and 6.0 million tons from total stocks of anchovies and sardines for the years 1950-53, 1954-60, and 1961-65 respectively. The proportion of this natural loss due to predation by game fish can be estimated by making assumptions on feeding rates and game fish biomass. To find likely maximum values for these ratios, it was assumed that combined rates of exploitation on game fish for all fisheries were near 5 percent annually, that game fish consume 5 percent of their body weight per day in anchovies and sardines, and that game fish feed 200 days per year on the anchovies and sardines. The estimated proportions of mortality are 100 percent, 50 percent and 25 percent for the periods 1950-53, 1954-60, and 1961-65 respectively. For the earlier years, food supply may have indeed been a limiting factor. The assumptions and absolute values of the ratios are relatively unimportant, invariably leading to the conclusion that the influence of game fish on forage supply should have decreased rather significantly between the periods 1950-53 and 1961-65. This contradicts the suggestion that the forage supplies in 1950-53 were influenced by game fish to the same extent as those in 1961-65 as suggested by similar slopes and scatter of points in the anchovy-sardine biomass and game fish CPUE relationship (Fig. 35).

In summary, the trends in forage biomass and game fish availability are probably coincidental. The evidence is too incomplete at this time to demonstrate the degree of dependency of game fish on forage supplies.

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Transport of Heavy Chlorinated Hydrocarbons in the Atmosphere

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■ Fluxes of aerosol polychlorinated biphenyl (PCB, 54% chlorine mixture) ranging from 2×10^{-9} to 9×10^{-7} (average: 3×10^{-7}) g m^{-2} day^{-1} were measured at La Jolla, Calif., during February and October 1972. A model for mesoscale aerosol transport which treats the plume as a superposition of Gaussian-shaped puffs diffusing isotropically in the plane of the horizon was used with the assumption that deposition occurs irreversibly to compute source strength, aerosol half-life, and isopleths of deposition flux. Hourly wind velocity and daily deposition flux measurements made during a one-month period were used to calibrate the model, and a second month of data provided a check for the predictive capacity of the method. On the basis of flux measurements and model calculations, arguments are presented for most dry deposition of aerosol PCB introduced into the troposphere to occur within 100 km of the source.

Polychlorinated biphenyls (PCB) are used to plasticize paints, adhesives, and plastics and are among the most refractory of synthetic organic chemicals. In Southern California, where this study took place, open burning has been largely supplanted by landfill disposal, but high temperatures in landfills as well as weathering of products containing PCB could contribute to the emission of this material as an aerosol. Volatilization of PCB used as a fireproofing agent is also a possible source of aerosol since about 400 fires occur daily in Los Angeles, of which 5% are structure fires. The manufacturer of PCB in the U.S. voluntarily restricted sales of PCB to closed system applications (heat transfer, dielectric, lubricant, and hydraulic fluids) in 1971. This action is not likely to reduce the emission of aerosol PCB until the service life of the products involved has expired and they are safely disposed of.

Distribution of Sources and Sinks and Relationship Between Deposition Flux and Aerial Concentration

Location of Sources. A correlation between measured fluxes and the component of the wind trajectory in the assumed direction of the source weighted by the reciprocal of the wind speed has been shown (*1*). This correlation supports the hypothesis that the location of the source of aerosol PCB is in the Los Angeles area. The susceptibility of the flux data to a rectification by an empirical, qualitative calculation suggests that a more quantitative model would be capable of predicting source strength, half-life in the atmosphere, and isopleths of the deposition flux from the same type of wind velocity and deposition flux data. Physical considerations and experimental observations which are fundamental to such a quantitative aerosol transport and deposition model are developed in the following paragraphs.

Procedures for flux measurement and analysis have been described (*1*) which involve the use of 0.17 m^2 mineral oil-coated glass deposition plates. The deposited chlorinated hydrocarbons (CHC) are scavenged from the mineral oil on an active silica-gel column, eluted from the column with *n*-hexane, concentrated under vacuum, and analyzed by gas chromatography with electron-capture detection.

Half-Life of PCB in Soil and Secondary Emission. To invoke the principle of conservation of mass in a practical aerosol transport model, the most important sources and sinks must be identified. In particular, the reemission of material which has deposited on the earth's surface (secondary emission) must be accounted for.

If the flux of PCB (54% chlorine mixture) over the last 30 years is approximated by a linear increase from zero to that found in 1972, the total input to the soil at La Jolla would be about 3×10^{-3} g m^{-2}. At undisturbed uneroded gently sloping locations near the aerosol sampling site, the amount of PCB in the upper 10 cm of soil was measured at an average surface concentration of 1.6×10^{-3} g m^{-2} (range, 0.5×10^{-3} to 3.0×10^{-3} g m^{-2} from 12 cores). Steep slopes and exposed ridge-crests yielded low surface concentrations while alluvial deposits were rich in CHC only if they had a high "fines" (passing a 100-μm screen) content. The concentration of PCB in the soil at a depth of 10 cm was typically 0.2 of the concentration at the surface of adobe cores and as high as 0.8 for more permeable soils. It is apparent that CHC is being transported by hydraulic action vertically down into the ground.

Given the linear increase of deposition flux with time assumed in the previous paragraph and the observed surface concentrations, the half-life of PCB in the top 10 cm of soil can be calculated. Equate the time rate of change of surface concentration, dC_2/dt, with the assumed input from aerosol, k_2t, minus the concentration-dependent term describing the disappearance via the combined agencies of secondary emission and leaching downward, k_1C_2, to give $dC_2/dt = k_2t - k_1C_2$ which is solved by $C_2(t) = k_1^{-1}k_2t[1 - \exp(-k_1t)]$. With $k_2 = 6 \times 10^{-6}$ g m^{-2} yr^{-1} and $C_2(t = 30\text{ yr}) = 1.6 \times 10^{-3}$ g m^{-2}, k_1 is calculated to be 0.114 which corresponds to a half-life of PCB in the top 10 cm of soil due to leaching and secondary emission of 6 years.

This approximate result agrees substantially with the 10-year half-life found by Nash and Woolson (*2*) for the disappearance of DDT from experimental plots which were provided with good drainage. Residence times in soil of DDT and PCB should be approximately equal since the two compounds have similar solubilities, vapor pressures, and adsorption properties on solid surfaces. Woodwell et al. (*3*) divided the amount of DDT retained in soils in the continental U.S. by the annual rate of application to arrive at an estimate of the lifetime in the soil of 4.5 years. However, our results and those of

Tarrant and Tatton (*4*) show that soil concentrations of CHC in areas not subject to direct application are *increasing* so that the assumption of a steady state cannot be made. Since the disappearance of CHC from soil is due to leaching as well as volatilization or mobilization on aerosol particles (secondary emission), the half-life for secondary emission alone should be longer than 10 years.

If the secondary emission half-life is sufficiently long, the process of deposition of aerosol on the ground can be considered to be irreversible. Our assertion that secondary emission can be neglected when considering a primary aerosol source 100 km distant is also based on observations during easterly winds of PCB fluxes less by a factor of 500 than during winds from the direction of Los Angeles (Figure 1). If no primary sources are located east of the measuring site, then any PCB flux during easterly winds should be attributable to secondary emission. Low fluxes during easterly winds are consistent with the earth's surface as a good reflector *or* a good absorber of aerosol PCB. Since a substantial portion of the time integrated deposition of PCB is accounted for in the soil, the most reasonable interpretation of these data is that the earth's surface can be treated as a good absorber of aerosol PCB.

Near a source, where concentrations in the soil are high, it is reasonable to expect that secondary emission could become appreciable. A convenient model for a primary source surrounded by a region of diffuse secondary emission is a Gaussian distribution of source strength.

Deposition Velocity, Deposition Flux, and Atmospheric Stability. A relation between the concentration of material in the air and the flux of material from the air to the earth's surface must be found to construct a transport model. If turbulence in the atmosphere were homogeneous in space and time, and if we are far from the source so that the aerosol size distribution is relatively constant in space and time, then the assumption that the deposition velocity, V_d, remains constant would provide such a relationship: Flux, $F = V_d\chi(z = 0)$, where z is altitude and $\chi(z = 0)$ is the ground level aerial concentration. However, a synoptic knowledge of both $\chi(z = 0)$ and turbulence conditions will actually be required to account for the inhomogeneity that is present in the atmosphere.

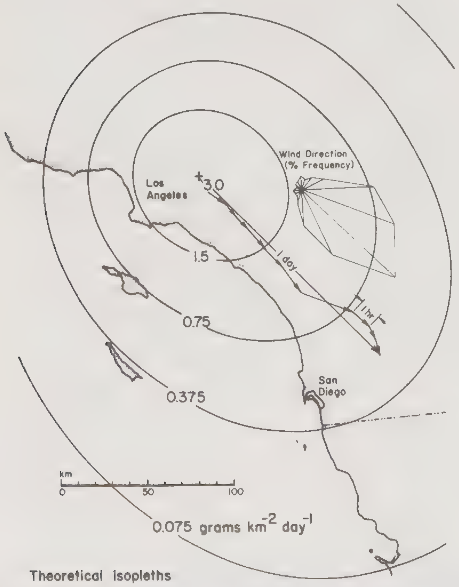

Figure 1. Model parameters for calculation of this series of isopleths: deposition coefficient, $k = 0.146$ h^{-1}; exponential dispersion parameter, $n = 0.25$; linear dispersion parameter, $c = 14.7$; source strength, $Q = 3.0$ kg h^{-1}

Wind data for October 1972 used, and isopleths reflect average for whole month. Isopleths for February 1972 are much the same. Emission from San Diego not included in calculations. If position of model source displaced more than 35 km in any direction from position shown, constant flux fits measured fluxes better in least-squares sense than transport model predictions

Within a few kilometers downwind of a source under stable conditions, deposition velocity decreases with distance from the source (*5*). This is probably due to depletion from the plume of large ($\gtrsim 10$ μm) particles whose gravitational fall velocity is significant in comparison to the deposition velocity resulting from turbulent motion. However, a submicron particle, even under stable conditions, can have a deposition velocity which is 5–50 times faster than its sedimentation velocity, V_s, in the absence of turbulence. For unstable conditions, V_d is two to three orders of magnitude larger than V_s for 1-μm particles, and the data show too much scatter to detect any decrease of V_d with distance from the source. Values for V_d computed from dispersion models and material balance considerations (*5*) are larger than V_d determined directly from wind tunnel tests (*6*). For downwind distances of more than a few kilometers, sedimentation due to gravity is insignificant in comparison to the influence of turbulence on deposition velocity.

Concurrent flux and ground level concentration measurements were made to determine the effect of various states of turbulence on deposition velocity. To be above the laminar boundary layer which would be expected to be depleted by deposition, ground level aerial concentrations were measured at $z = 10$ cm above a flat surface by drawing air through a 10 mm diam × 75 mm long column of oil-impregnated glass wool in series ahead of an oil-filled impinger. CHC was recovered from the mineral oil by the same methods used for the flux measurements. Sampling periods of 4–8 h duration were made to coincide with the presence of either stable (inversion, stratified) or unstable (lapse, well-mixed) atmospheric conditions. Stable conditions occurred during night and morning hours and were frequently accompanied by a stratum of smog about 500 m thick over the ocean trapped by a surface-based inversion. Unstable and neutral conditions in which the atmosphere was being mixed by thermal convection or mechanical turbulence occurred in the afternoon and were evidenced by strong insolation and brisk sea breezes (3–8 m s^{-1}). The results of these measurements are shown in Table I.

When the atmosphere is stratified, high ground-level concentrations occur together with low deposition velocities. Conversely, when the atmosphere is well mixed, low $\chi(z = 10$ cm) accompanies large V_d. The deposition velocities measured for PCB were similar to those found for ^{131}I (*7*) and for uranin particles by Islitzer and Dumbauld (*5*) and show the increase with instability noted in the latter work. Islitzer and Dumbauld used particles with a diameter of about 1 μm which is comparable to the average mass mean diameter of Los Angeles smog particles (*8*).

Although changes in atmospheric stability strongly influence the vertical profile of aerial concentration in a plume, the decay or onset of turbulence does not affect the quantity of material in the air above a unit area:

$$\chi_{vi} = \int_0^\infty \chi(z)dz$$

Table I shows that ground level concentration and deposition velocity are both much more sensitive to the prevailing state of atmospheric turbulence than is the deposition flux. A second set of flux measurements was made to test the extent to which changes in $\chi(z = 10$ cm) and V_d with changing turbulence conditions might compensate to give a flux which is approximately independent of turbulence. The occurrence of this set of circumstances is requisite for the validity of our approximation, $F = k\chi_{vi}$, that deposition flux is proportional to the vertically integrated aerial concentration. This approximation avoids the difficulty of quantifying atmospheric turbulence and reduces the transport problem to two dimensions.

A consecutive series of flux measurements was made with the duration of each measurement confined to periods of stationary turbulence. That is, a new sampling period was begun each time a change in stability or state of mechanical turbulence was observed in the atmosphere. The average of six PCB deposition flux measurements made during unstable conditions was 15.3×10^{-9} g m^{-2} h^{-1}, while the average flux for six stable periods during the same week of observations was 9.3×10^{-9} g m^{-2} h^{-1}. Some of the difference between fluxes during stable and unstable periods is likely to be due to noncompensating effects of turbulence on $\chi(z = 10$ cm$)$ and V_d. However, stable periods during which winds are slight to calm can be expected to yield lower fluxes since depletion of the plume by deposition is not made up for by advection. This set of measurements therefore shows the maximum influence that turbulence can have on deposition flux. A 24-h sampling period was chosen to minimize possible error caused by diurnal variation of atmospheric stability when the result of this sampling was to be compared with model calculations based on the approximation that flux is independent of turbulence.

Wind velocities were measured at Montgomery Field which is located on level terrain about 10 km east of the flux receptor site. Hourly wind velocities to be used in the transport model calculations were averaged to obtain mean wind bearings for October and February 1972 (data deposited with the ACS Microfilm Depository Service). These bearings were close to those computed from U.S. Naval Synoptic Surface Meteorological Observations (SSMO) (*9*) which combines data from vessels in the region 31° to 34° North and the coastline to 120° West: for October, 304.6° vs. 305.6° (SSMO) and for February, 323.4° vs. 322.9° (SSMO). These results indicate that the wind field in the neighborhood of the measuring site is free from terrain-induced distortions and that velocities measured there are representative of winds over the whole Southern California coastal and nearshore region.

Gaussian Puff Deposition Model

The assumptions and approximations that are contained within the model are: (1) The source is of constant strength and Gaussian shape, (2) eddy diffusivity is isotropic in the horizontal plane, and (3) deposition flux is proportional to the vertically integrated aerial concentration (the amount of material in the air above a unit area):

$$\text{Flux, } F(x, y) = k \int_0^\infty \chi(x, y, z)dz = k\chi_{vi}(x, y)$$

Deposition flux is assumed to be independent of other factors such as wind velocity, horizontal wind shear, temperature and lapse rate.

To describe the two-dimensional concentration of material in a puff originating at the point $r = 0$ at time $t = 0$ diffusing isotropically in the plane of the horizon and falling irreversibly from the atmosphere, the expression

$$\chi_{vi}(r, t) = \frac{Q}{2\pi\sigma^2} e^{-kt} e^{-r^2/(2\sigma^2)} \qquad (1)$$

was employed where Q is the quantity of material in the puff, σ^2 is the dispersion, k is the deposition coefficient of assumption 3, and r is the distance from the center of mass of the puff (Lagrangian coordinate).

Table I. Ground Level Concentration, $\chi(z = 10$ cm$)$, Deposition Flux, and Deposition Velocity of Aerosol PCB Measured During Various Atmospheric Stability Conditions

Mo./day, 1973	Wind speed, m/s (stability)	Ground level concn, (g/m^3) × 10^{-9}	Flux (g/m^2 h) X 10^{-7}	V_d, cm/s
3/28	2.5 (Neutral)	0.45	0.24	1.5
3/2	1 (Strong surface-based inversion)	14.0	1.6	0.31
3/15 (a.m.)	1 (Weak surface-based inversion)	4.8	0.76	0.44
3/15 (p.m.)	4 (Lapse)	1.4	1.5	3.0
4/6	6.5 (Lapse)	1.26	0.46	1.0

When $\sigma^2 = 2\,Kt$ (with K the Fickian eddy diffusivity), this Gaussian distribution (Equation 1) provides a solution to the gradient diffusion equation:

$$\frac{\partial \chi_{vi}}{\partial t} + k\chi_{vi} + K\left(\frac{\partial^2 \chi_{vi}}{\partial x^2} + \frac{\partial^2 \chi_{vi}}{\partial y^2}\right) = 0,\ x^2 + y^2 = r^2$$

which requires that the time rate of change of χ_{vi} be balanced by the deposition flux, $k\chi_{vi}$, and by eddy diffusion, $K\nabla_2^2\chi_{vi}$.

The Gaussian distribution (Equation 1) also serves as a basis for many successful plume diffusion models in which the dispersion is not limited to a linear dependence on t. Based upon an interpolation formula for the Lagrangian velocity correlation coefficient, Sutton (*10*) derived the expression

$$\sigma^2 = \frac{1}{2} C^2([u]t)^{2-n},\ (n \text{ and } C \text{ constant, } 0 < n < 1) \qquad (2)$$

for the dispersion of a Gaussian-distributed cluster of diffusing material. The time over which the instantaneous wind, $u(t)$, was averaged to obtain the mean speed, $[u]$, was long enough to ensure that $[u]$ would represent a virtual steady flow.

A transport model that can take deviations from steady flow into account is more capable of predicting the dispersion of pollutant plumes than one that does not. Consider the dispersion, σ_1^2, of a puff after a time $2\Delta t$ with wind speed (u) compared to the dispersion, σ_2^2, which would result after time Δt at speed $(2\,u)$ followed by an hour of calm. If the wind speed were to be averaged over the whole time period $2\Delta t$, the predicted dispersion would be the same for both cases. When the eddy diffusion is considered to take place in two successive intervals of length Δt, the predicted dispersions for the two cases would be

$$\sigma_1^2 = 2(C^2/2)(u\Delta t)^{2-n} \text{ and } \sigma_2^2 = (C^2/2)(2\,u\Delta t)^{2-n}$$

That $\sigma_2^2 > \sigma_1^2$ is reasonable since the higher wind speed in case 2 could be associated with greater atmospheric turbulence and eddy diffusion.

An anemometer was observed for several minutes to estimate the average over this time period of the wind speed and direction. Velocities were found in this way each hour, and the results of each measurement were presumed to approximate the mean velocity which would result from an average taken over the whole hour. Hourly velocities are summed to show a typical daily trajectory in Figure 1.

The spreading of each puff in the plume was considered to have taken place during a succession of hour-long intervals.

Within each interval the eddy diffusion was described by the Sutton expression for the dispersion of the distribution of material. The increase in the dispersion of the puff during the ith hour due to effective eddies is

$$\sigma_i^2 = \frac{1}{2} c^2 (r_i)^{2-n} \tag{3}$$

where $r_i = u_i \Delta t$ is the trajectory length for the ith hour. A lower-case c is used to distinguish the virtual eddy diffusion coefficient used here (for $\Delta t = 1$ h) from C in Equation 2 which applies for $\Delta t >$ (source to receptor transit time, h hours). For the dispersion of a puff which has traveled the distance $R_h = \Sigma_{i=1}^{h} (r_i)$, the expression

$$\sigma^2(R_h) = \sum_{i=1}^{h} \sigma_i^2 + \sigma_o^2 \tag{4}$$

was used where σ_o^2 accounts for the finite size of the source.

Equation 1 and assumption 3 give for the deposition flux from a puff

$$F(r, t) = \frac{kQ}{2\pi\sigma^2} e^{-kt} e^{-r^2/(2\sigma^2)} \tag{5}$$

which satisfies $\int_0^\infty \int F(r, t) 2\pi r dr dt = Q$. (All that is emitted eventually is deposited on the earth.)

Wind velocity measurements made 15 m above the ground best represent the mean motion of a cloud released near the surface (*11*). Since wind velocities for this work were observed at only 7 m elevation above the ground, a parameter, α, was introduced which was applied to the observed wind speeds to yield larger effective speeds: $u_i(\text{eff}) = \alpha u_i(\text{obs})$.

Surface wind velocities and directions were measured hourly throughout the fallout sampling period and for 4 days (96 h) preceding the first 24-h measuring period. A puff of material containing Q grams of pollutant was assumed to have been emitted each hour. The lifetimes, positions, and trajectory lengths for 96 puffs emitted prior to each hour of measurement were computed to find the contribution of each puff to the total hourly deposition flux. The hourly fluxes were then totaled to give computed daily fluxes which could be compared with the measured daily fluxes.

After physically plausible initial values were chosen for the various parameters, each parameter was varied in turn to minimize δ = (sum of squares of the differences between measured and predicted fluxes). The variation of the model parameters was repeated until no further improvement could be made in the least-squares fit of the predicted to measured fluxes. The source strength, Q (g h^{-1}) was fixed by the requirement that the monthly average measured and predicted fluxes should be equal.

The value of the deposition coefficient, $k = 0.15$ h^{-1}, which minimized δ was within 5% of the value of k which caused the source strength to be a minimum while still predicting the correct monthly average flux. The source strength predicted by the model would be little changed by the requirement that the deposition coefficient be chosen to reproduce the monthly average flux with the smallest possible source.

The optimum (δ minimized) value for the exponential horizontal dispersion parameter, $n = 0.25$, lies in the midst of other experimental results and is equal to that found by Sutton in his original measurements. This result could be expected since this model is a straightforward adaptation of the Sutton model for variable wind velocity. Minima with respect to δ were found for the virtual diffusion coefficient and the wind speed scaling parameter at $c = 14.7$ and $\alpha = 1.8$. Model predictions and flux data are shown in Figure 2.

To compare the crosswind dimensions of the plume predicted by this model with dispersions measured during other atmospheric transport experiments, a computation of concentrations in various parts of the plume was performed using the parameters optimized by the iterative procedure described above. Experimental wind speeds were used in this concentration calculation, but hourly variations in wind direction were ignored. The crosswind profiles of this hypothetical "straightened" plume are shown in Figure 3. The influence of large-scale (greater than about 20 km radius of curvature) eddies or meanders on the plume spreading was separated from smaller-scale eddy diffusion effects in this computation of crosswind dispersion to provide a more realistic comparison with measurements made of plumes from noncontinuous sources. From Figure 3, the predicted variance of the crosswind concentration at 120 km, which is the distance from Los Angeles to La Jolla, is 69 km with the variance of the source (source diameter) set at its optimized value of 10 km. These dimensions compare favorably with published experimental values (*12*) which fall in the range 30–80 km. Although there was a rapid degradation of the least-squares fit of calculated to measured fluxes (increasing δ) when σ_o was increased beyond 20 km, only a slight increase in δ was noted when the model source was contracted to a point.

Eddies in the horizontal plane larger than $O(u_i \Delta t \sim 20 \text{ km})$ are explicitly accounted for from our knowledge of hourly wind velocities. Sutton's theory, together with the assumption of steady flow, would yield $\sigma^2 = \frac{1}{2} C^2 R_h^{2-n}$ which implies that the scale of effective eddies would continue to increase as trajec-

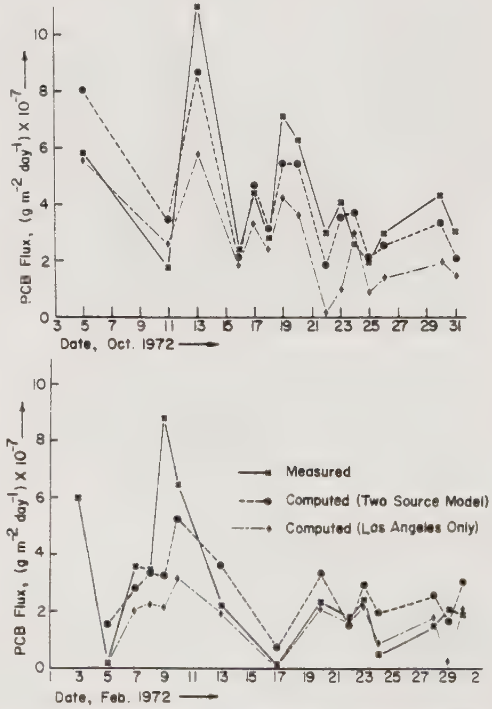

Figure 2. Best fit to measured flux data achieved with Los Angeles having source strength of 7.0 times that of San Diego

Source strength which must be assigned to Los Angeles to reproduce correct monthly average measured flux was 3 kg h^{-1} 54% chlorine PCB for October 1972 and 2.4 kg h^{-1} for February 1972. Other model parameters used in computations were $n = 0.25$, $c = 14.7$, $k = 0.146$ h^{-1}, and the initial source diameters, σ_o, were 10 km for Los Angeles and 1 km for San Diego. October data used to calibrate model, and values found in this process used to compute model predictions for February tories lengthen. Equation 4 allows the size of effective eddies to be limited to less than $O(u_i \Delta t)$.

A thinner planetary boundary layer exists over the smoother ocean so that winds observed from ships are closer to geostrophic than measurements made at land stations. Thirty-year mean surface winds at Southern California stations in rougher terrain than Montgomery Field (U.S. Weather Bureau data) reflect the influences of the local topography and show a generally more onshore and less geostrophic flow than the ship-based SSMO data. Since model predictions using the Montgomery Field data (which are similar to ship-based observations) correlate well with measured pollution levels, most of the pollutant transport 120 km distant from the source must occur above the slower moving surface layer which is of the order of tens of meters deep and is directed more nearly along the generally onshore gradients of pressure.

Terrain-induced inhomogeneities in the wind velocity field smaller than the cross-wind plume dimensions (about 50 km) are anticipated to be accounted for in the model by a horizontal dispersion which is larger than would be found for locations (at sea, for instance) having smoother terrain. Inhomogeneities that persist after spatial averaging over a scale of ~50 km would influence the trajectory of the plume centerline and cause predictions of the source location based on a mean wind field with straight and parallel streamlines to be in error. Inspection of the spatially smoothed contours of the Southern California coast and inland mountains allows an estimate of this error of no more than about 50 km in the crosswind direction. However, it was the purpose of this study to discover the atmospheric residence time of aerosol PCB and the strength of the source rather than its accurate location which is better accomplished by a grid of receptors nearer the source (*13*).

Implications of Transport Model Results

Residence Time in Atmosphere. The deposition coefficient, $k = 0.15\ \mathrm{h}^{-1}$, which provides the best least-squares fit of model predictions to measured fluxes, corresponds to an atmospheric half-life for PCB of 4.6 h. Since this result is considerably different from the 4-year time constant assumed for DDT by Woodwell et al. (*3*), the following considerations are presented to support the contention that the atmospheric half-life of surface-released aerosols whose deposition at the earth's surface is largely irreversible is of the order of hours or at most a few days. Factors which inhibit reemission of material deposited from an aerosol or vapor state are low vapor pressure or high affinity for solid surfaces or for solution. The last factor would be active in the case of sulfur dioxide for which Meetham (*14*) found an atmospheric half-life of between 8 and 10 h using deposit gauge data and estimates of emission during coal burning.

We can approximate the integral in assumption 3 as:

$$F = k \int_0^\infty \chi(z) dz \approx k\chi(z = 0)z_m$$

where z_m is a suitable height above the surface. Using the definition of deposition velocity, $F = V_d \chi(z = 0)$, we get $k \approx V_d/z_m$. During unstable conditions the deposition velocity of PCB is in the range 1–4 cm s^{-1}, and z_m is the thickness of the atmospheric mixed layer, which is estimated by the heights of cumulus clouds at 1–3 km. These considerations place k in the range 0.01–0.14 h^{-1}. For stable atmospheric conditions, V_d is about 0.4 cm s^{-1}, and z_m is the depth of the surface-based inversion layer. The smog layer trapped by the surface-based inversion was estimated to be 300–800 m thick on the days when V_d was measured. Thus, k should be from 0.02 to 0.05 h^{-1} during stable conditions. If it should happen that the concentration of PCB remains constant throughout the depth of the mixed layer during stable conditions, then the smallest value for k would be about 0.005 h^{-1} for a half-life of 140 h. Such a long half-life would prevail only if the atmosphere never becomes turbulent. A constant flux equal to the experimental average flux fits the data better in a least-squares sense than model predictions using $k = 0.005\ \mathrm{h}^{-1}$. In addition, a source strength of over 250 metric tons yr^{-1} of the 54% chlorine grade PCB would be required from Los Angeles for this model to predict the correct measured average flux when this long half-life is assumed. Five percent of the U.S. population reside in the Los Angeles area. If the U.S. production of about 5×10^3 metric tons yr^{-1} of (54% Cl) PCB is allocated on a per capita basis, only about 250 metric tons yr^{-1} would be used in Los Angeles. A half-life in the atmosphere as long as six days would imply that dispersal into the atmosphere is the principal fate of PCB. Current estimates (*15*) are that landfill disposal accounts for the majority of waste PCB.

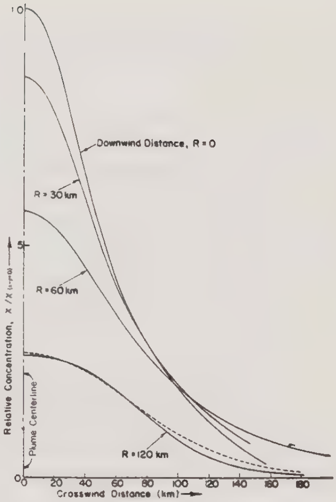

Figure 3. Predicted cross-wind plume dimensions at various distances from source

One month of wind speed data used to generate average concentration distribution. Instantaneous concentrations can be considerably different from average. Profile at $R = 0$ different from that of source since diffusion in wind direction allows puffs whose centers have been moved downwind to continue to contribute to concentration at $R = 0$. Broken line is Gaussian with $\sigma = 69$ km

Relative Importance of Rain Scavenging and Dry Deposition. The concentration of PCB and chlorinated pesticides in two samples of rainwater from squalls which approached the sampling site from the seaward (southwest) direction was less than our detection limit of 2×10^{-12} g ml^{-1} (*16*). However, dry deposition measurements made during and immediately after the passage of the front yielded CHC fluxes which were also less than our detection limit of 10^{-9} g m^{-2} h^{-1}. These low values are reasonable in light of the fact that during southwest winds, no sources of aerosol are located upwind of the measuring site. Although these data are consistent with the conclusion (*1*) that aerosol transport of heavy CHC is a mesoscale rather than a global phenomenon, it cannot resolve the relative importance of dry deposition and rain scavenging for any location other than La Jolla: A 50 cm yr^{-1} rainfall containing 10×10^{-12} g ml^{-1} would contribute only 5 g km^{-2} yr^{-1}, whereas dry deposition is responsible for a PCB flux at La Jolla based on average measured fluxes during October and February 1972, of 180 g km^{-2} yr^{-1}.

We can write Raoult's law for sparingly soluble compounds as $P/C = P_o/C_o$ where P is the vapor pressure of the compound over a solution of concentration C, and P_o and C_o are the vapor pressure of pure compound and its solubility in water, respectively. DDT has a solubility of 2×10^{-9} g ml^{-1} and a vapor pressure of 10^{-6} mm Hg (*17*) which is equivalent to 2×10^{-5} g m^{-3} if the vapor behaves as a perfect gas. Consider a concentration of 10 ml m^{-3} of rain falling continuously at a flux of 1 l. m^{-2} h^{-1} (360 in./year) through a 1-km deep stratum of atmosphere containing DDT vapor. For this situation, if equilibrium partitioning between phases occurs, Raoult's law predicts that one 10^3 part of the total DDT be present in the liquid and that the time constant for removal of DDT vapor from the atmosphere by rain is 10^4 h.

The flux of particulate material onto the glass plates averaged 10^5 times the CHC flux, but no correlation was found between CHC and particulate fluxes. Bidleman and Olney (*18*) observed that a negligible fraction of airborne CHC was captured on a glass fiber filter capable of removing 98% of particulates having diameters greater than 0.03 μm. This is an indication that airborne CHC exists primarily in the vapor state. However, high PCB fluxes were strongly correlated with smoggy conditions and the deposition of black-colored particles. Chlorinated pesticide fluxes reached their maximum levels on days when brown-colored particles were deposited. In urban areas, CHC could well be more strongly associated with the surfaces of soot particles (*19*) than with the more hydrophylic particles found at remote locations.

From measured collision (target) efficiencies (*20*) for rain drops falling through clouds of smaller particles and from experimental raindrop size distributions, Chamberlain (*21*) has calculated washout coefficients from which the time required to diminish the concentration of particulates in the air to one-half the original concentration can be found. For 2.0-μm diam particles with density 2.0 in rain falling at 1 mm h^{-1}, this half-life is 1.9 h. A 1-μm diam particle under similar conditions has a half-life of about 20 h. Most atmospheric aerosols have size distributions which account for only a small percentage of total surface area on particles larger than 1 μm [5% for Los Angeles aerosol (*8*)]. In his conclusion to the chapter on precipitation scavenging in "Meteorology and Atomic Energy" (*22, 23*), R. J. Engelmann states, "In the case of particles smaller than 1 micron, it is generally agreed that washout by rain is insignificant."

The times required for washout by rain of CHC in the vapor state or adsorbed on submicron particles are as long or longer than the time attributable to the process of dry deposition. Since precipitation occurs only a fraction of the time (1.8% in Southern California) and since dry deposition takes place continually (even during precipitation), then dry deposition is the major mechanism for transfer of heavy chlorinated hydrocarbons from the atmosphere.

Conclusions

The half-life in the troposphere of aerosol, high-boiling chlorinated hydrocarbons released near the surface is about 5 h. This corresponds to a downwind distance at which the quantity of material remaining in the plume is reduced by one-half of less than 100 km. Consequently, the atmosphere cannot be considered to be a large reservoir for these pollutants. The source strength for emission of aerosol PCB (54% chlorine mixture only) of metropolitan Los Angeles is calculated to be 20 metric tons/year (based on February 1972 deposition flux and wind data) and 30 metric tons/year (using October 1972 data). Inspection of theoretical isopleths (Figure 1) calculated with a two-dimensional aerosol transport and irreversible deposition model from single-point wind data indicates that about 30% of the emitted PCB is deposited in the Pacific Ocean in the Gulf of Santa Catalina.

Dry deposition accounts for the majority of CHC fallout. Measurements of CHC concentration in rainwater have been reported which were made with a receptor left out for weeks or months (*24*). These measurements are likely to be biased by the dry deposition which would also fall on the collecting surface. In fact, Tarrant and Tatton (*4*) found that the influx of organochlorine pesticides in rain fall was not sufficient to account for the observed increase with time of the concentration of these compounds in untreated soil plots. These rainfall concentrations are crucial because they have been used along with the questionable assumption that aerosol CHC is uniformly distributed over the globe to predict the flux of CHC into the world's oceans (*3*).

Land areas are good absorbers of aerosol CHC. Except for agricultural soils subject to heavy pesticide application, land areas are capable of adsorbing a great deal more airborne CHC before the rate of secondary emission balances the deposition flux. This conclusion, of course, holds only for compounds with low (10^{-4}–10^{-5} mm Hg or less) vapor pressures. Low boiling compounds are likely to have much longer residence times in the atmosphere, be dispersed over much wider areas, and find their way more rapidly to the oceans. A half-life of hours or a few days for CHC in the troposphere would lead to severe local contamination of land areas (~100-km radius about the source) before atmospheric transport could be expected to produce serious contamination on a global scale. On the other hand, a pollutant entrained in an ocean current could easily have started its journey from an urban area as an aerosol. Global transport via ocean currents is the most logical explanation for the presence of most of the heavy CHC which has been detected in the ocean at places remote from known sources of contamination.

An annotated listing of the computer program in Fortran that was developed for the computations of deposition fluxes from a plume of superposed Gaussian puffs and an additional figure have been deposited with the ACS Microfilm Depository Service.

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Supplementary Material Available. *An annotated listing of the computer program in Fortran, wind direction and speed data, and an additional figure will appear following these pages in the microfilm edition of this volume of the journal. Photocopies of the supplementary material from this paper only or microfiche (105 × 148 mm, 24× reduction, negatives) containing all of the supplementary material for the papers in this issue may be obtained from the Business Operations Office, Journals Department, American Chemical Society, 1155 16th St., N.W., Washington, D.C. 20036. Remit check or money order for $4.00 for photocopy or $2.50 for microfiche, referring to code number ES&T-76-1223.*

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DDT AND ITS METABOLITES IN THE SEDIMENTS OFF SOUTHERN CALIFORNIA

JOHN S. MACGREGOR[1]

ABSTRACT

To assess the degree of DDT contamination in the marine sediments off Los Angeles, 103 stations in the Pacific Ocean off southern California were sampled in July and August 1971 for DDT and its metabolites, DDD and DDE. Heavy contamination of bottom sediments in this area was expected because of large amounts of DDT that have entered the ocean through the Los Angeles County sewer system as waste from a DDT manufacturing plant.

From the data acquired, it was estimated that there were about 200 metric tons of DDT, DDD, and DDE in the sediments in an area of 14 square nautical miles near the sewer outfalls and 300 metric tons in the entire 911 square nautical mile area sampled. The heaviest concentrations of total DDT were distributed in the relatively shallow-water area on the Palos Verdes shelf to the northwest of the sewer outfalls in the general direction of the current flow.

Metabolism of DDT was inhibited in deepwater sediments. Ratios of DDE to DDT were low, and DDT was more abundant than DDE at some stations. In sediments from shallow-water stations, DDE exceeded DDT by more than 10 times.

The bottom of the ocean off Los Angeles, Calif., has been very heavily contaminated with the pesticide DDT owing to the discharge of wastes from a DDT manufacturing plant into the Los Angeles County sewer system over a period of about 20 yr ending in 1970 (MacGregor 1974).

The amount of DDT which entered the ocean through the Los Angeles County sewer system was estimated at 250 kg/day. Following the cessation of DDT discharges by the manufacturer, the amount entering the ocean dropped to 45 kg/day in December 1970 and to 11 kg/day in October 1971. Most of these later discharges resulted from sewer cleaning operations which stirred up old deposits of DDT in the sewer lines. The discharges resulting from the cleaning operations were primarily DDD and DDE, metabolites of DDT, while the earlier discharges were primarily DDT.

Because there has been a great deal of speculation about the fate of DDT and other toxic chemicals released into the environment by man (Woodwell et. al. 1971; National Academy of Sciences 1971), this investigation was undertaken to determine the areal distribution and fate of these chemicals in the bottom sediments in the ocean off Los Angeles.

MATERIALS AND METHODS

The bottom sediments were sampled from a grid of 103 stations between lat. 33°30′ and 33°58′N and long. 118°00′ and 118°44′W (Figure 1). The stations were designated by four-digit numbers, the first two indicating minutes north

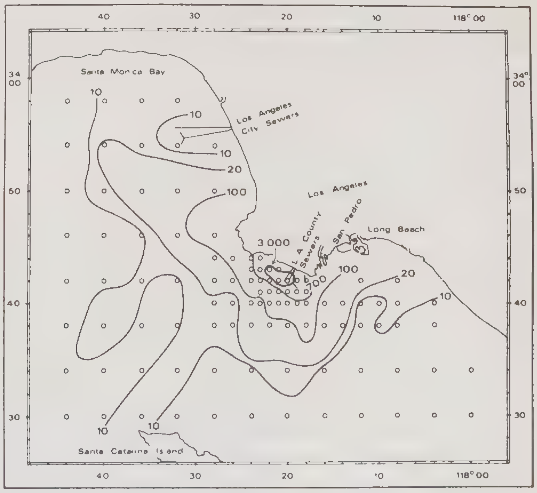

FIGURE 1.—Distribution of total DDT in milligrams per square meter of bottom in the sediments of southern California. Total DDT ranged from 6,600 mg/m² of bottom at station 43-22 to 0.12 mg/m² at station 30-08.

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of lat. 33°N and the second two indicating minutes west of long. 118°W.

The samples were taken aboard the National Marine Fisheries Service RV *David Starr Jordan* between 26 July and 3 August 1971. The Shipek bottom sampler was used to obtain the samples of sediment. This device obtains a block of material equal to 400 cm^2 of bottom sediment to a depth of about 10 cm, or slightly more, in soft mud or to a depth of half as much or less in coarse sand.

Two samples were taken at each station in order to obtain an estimate of sampling error. The vessel was allowed to drift while the samples were being taken, so the sample pairs were taken in only approximately the same location. However, agreement in the various parameters between samples from the same station was good.

The samples were placed in aluminum foil-lined containers of approximately the same size as the sampling bucket and were quick-frozen. They were stored in a freezer until removed for analysis.

In most samples, DDT was confined to the top 2 or 3 cm of the sediment. At most of the stations where the sampler sampled to 10 cm, and at all of the stations where it sampled to a lesser depth, it appeared that all of the DDT under the 400 cm^2 had been sampled. In this study, therefore, DDT concentrations are given as the weight of DDT per unit area of bottom to a depth of 10 cm. In a few areas of rapid sedimentation, where the sampler sampled to about 10 cm depth, there were still significant amounts of DDT below 10 cm. Estimates for the amounts of DDT below 10 cm are based on core samples taken by other investigators in this area.

The bottom sediment samples were thawed and blended in a 1-gallon Waring[2] commercial blender. Before blending, small stones were removed from the few samples that contained them. Some samples contained a few small molluscs or brittle stars, but these were not removed. Measured amounts of distilled water were added to some of the drier (sandy) samples to facilitate blending.

A sample of 15 to 20 g of blended sediment was weighed onto a watch glass, dried to constant weight, and reweighed to obtain percent water in the sediment. This gave an index of bottom type ranging from 30 to 40% water for coarse sand to 60 to 70% water for fine silt.

A second sample weighing about 30 g was weighed into a 1-pint Mason jar for DDT determination. About four or five times as much Na_2SO_4 was weighed into the jar as a drying agent. The sediment and Na_2SO_4 were mixed using a stainless steel spatula, and the mixture was frozen. A cutting assembly was fitted to the jar, and the frozen mixture was thoroughly blended to a powder using an Osterizer blender.

About 5 g of the powder was weighed into a tared, large disposable pipet (Matheson super pipet) plugged with glass wool. The powder was extracted into a 15-ml graduated centrifuge tube with 5 ml of hexane and 5 ml of acetone. The extract was evaporated to dryness and redissolved in 1 ml of hexane. This sample was eluted through a super pipet filled with activated alumina (McClure 1972) using enough hexane to obtain a 6-ml sample.

This sample was reduced or increased in volume as required and injected into a model 402 Hewlett Packard gas chromatograph (GLC) with a Ni^{63} electron capture detector. The 6-foot glass column contained 4% SE-30/6% QF-1 on 100/120 mesh Supelcoport.

There was evidence of a polychlorinated biphenyl, Aroclor 1254, in all samples, but the DDT peaks were so dominant in the chromatograms that they generally obliterated any traces of other chlorinated hydrocarbons within their range. Only the six peaks representing the ortho-para and para-para forms of DDE, DDD, and DDT were quantified. "Total DDT" is used to designate the sum of these six analogs.

RESULTS AND DISCUSSION

Fifty-five correlations were obtained for 11 parameters to determine various DDT relationships. The 55 correlations were obtained for all 103 stations (Table 1, values above 1.000 correlation diagonal) and for 76 stations leaving out those 27 stations having total DDT readings greater than 100 mg/m^2 (Table 1, values below 1.000 correlation diagonal). For 100 observations a correlation coefficient of 0.254 indicates a probability of 0.01. Logarithms were used for total DDT and distance from outfall, arithmetic values for the other nine measurements.

There is a very high negative correlation between log total DDT and log distance from the

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[2] Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Correlation coefficients for 11 parameters relating to DDT and its metabolites in bottom sediments off southern California. Values above 1.000 correlation diagonal are for 103 stations. Values below diagonal are for 76 stations leaving out those 27 stations having total DDT readings greater than 100 mg/m². For 100 observations, a correlation coefficient of 0.254 indicates a probability of 0.01.

Parameter	Log total DDT	Log distance from outfall	Depth	Sample weight	% H_2O in sample	$\frac{p,p'\text{DDD}}{p,p'\text{DDT}}$	$\frac{p,p'\text{DDE}}{p,p'\text{DDT}}$	$\frac{p,p'\text{DDE}}{p,p'\text{DDD}}$	$\frac{o,p'\text{DDE}}{p,p'\text{DDE}}$	$\frac{o,p'\text{DDD}}{p,p'\text{DDD}}$	$\frac{o,p'\text{DDT}}{p,p'\text{DDT}}$
Log total DDT	1.000	−0.871	−0.253	0.221	0.157	0.142	0.144	0.281	−0.040	−0.272	−0.334
Log distance from outfall	−0.604	1.000	0.228	−0.095	−0.147	−0.032	−0.043	−0.238	0.016	0.332	0.334
Depth	0.078	−0.036	1.000	0.643	0.771	−0.443	−0.512	−0.572	0.315	0.168	0.095
Sample weight	0.245	0.041	0.761	1.000	0.743	−0.265	−0.341	−0.332	0.190	0.036	−0.151
% H_2O in sample	0.095	0.002	0.921	0.756	1.000	−0.315	−0.390	−0.396	0.228	0.019	−0.013
*p,p'*DDD/*p,p'*DDT	0.123	0.066	−0.418	−0.268	−0.325	1.000	0.909	0.297	−0.168	−0.194	0.556
*p,p'*DDE/*p,p'*DDT	0.100	0.040	−0.492	−0.366	−0.416	0.907	1.000	0.446	−0.208	−0.171	0.463
*p,p'*DDE/*p,p'*DDD	0.060	−0.075	−0.535	−0.418	−0.487	0.268	0.408	1.000	−0.289	−0.043	−0.011
*o,p'*DDE/*p,p'*DDE	0.190	−0.234	0.296	0.225	0.248	−0.151	−0.196	−0.273	1.000	0.021	0.113
*o,p'*DDD/*p,p'*DDD	−0.129	0.275	0.106	0.090	0.059	−0.177	−0.151	0.023	−0.024	1.000	0.130
*o,p'*DDT/*p,p'*DDT	−0.154	0.167	0.006	−0.127	0.025	0.630	0.537	0.084	0.068	0.060	1.000

Los Angeles County sewer outfalls ($r = -0.871$). Values ranged from 6,600 mg of total DDT/m² of bottom near the sewer outfalls to about 1 mg/m² at more distant stations.

The distribution of DDT was modified somewhat by currents which tended to deposit the DDT along the coast and to the northwest more than to the east (Figure 1). The apparent relation between total DDT and depth results from the fact that the sewers discharge into relatively shallow coastal waters and the sludge tends to remain there. The deeper waters are merely farther from the sewer outfalls and the areas along the coast favored by the currents.

McDermott et. al. (1974) took sediment samples from the Palos Verdes shallow-water shelf area in the vicinity of the sewer outfalls only. Their tables A-1 and A-4 give total DDT in parts per million dry weight from gravity core samples taken in 1972. I have contoured their data (Figure 2B) for the top 10 cm of sediment to compare with the 1971 data (Figure 2A) which has been converted to parts per million dry weight. Their 1973 data in their table A-5 represents parts per million dry weight of total DDT in the top 5 cm of Shipek samples taken in the same area (Figure 2C). In each of the 3 yr the patch of sediment representing more than 100 ppm. total DDT tends to retain its integrity fairly well as an oblong area stretching to the northwest of the sewer outfalls. The contours representing 10 to 100 ppm. seem to be expanding somewhat to the northwest and in 1973 to the southeast also.

At the Los Angeles County sewage disposal plant, most of the solids are removed by centrifuging, but the supernatant is pumped into the ocean along with the water from the settling tanks. This reduces the amount of particulate matter being discharged into the ocean. Nevertheless, quantities of relatively DDT-free particulate matter have been deposited on the Palos Verdes shelf since dumping of DDT into the sewer system was stopped. In time this could cause a change in the DDT profile of the sediments.

On the other hand, most of the shallow inshore areas along this section of coast tend to have sandy bottoms, and the silt bottoms in the vicinity of the sewer outfalls would appear to be unstable artifacts. Storms, tides, and currents could remove or deposit layers of bottom silts in this shallow-water area and further change the DDT profiles.

Based on the paired samples taken in 1971, the variation within a sampling area for one sample would be roughly plus 100% minus 50% at a one standard deviation level. For an average for two samples it would be plus 70% minus 40%. This could account for the differences in the distribuion of total DDT for the 3 yr. However, the similarities are much more striking than the differences.

High sample weight and high water content both indicate samples containing more silt, while lower weights and lower water content indicate samples containing more sand. Both of these measurements are related to depth, with the bottom in deep basins tending to be fine silt while shallow areas tend to be sandy. This tendency is masked in shallow-water areas where there are sewer outfalls which deposit large quantities of fine material in the shallower waters. This is indicated by the improvement of the correlation coefficients from 0.643 to 0.761 for sample weight and from 0.771 to 0.921 for percent water with

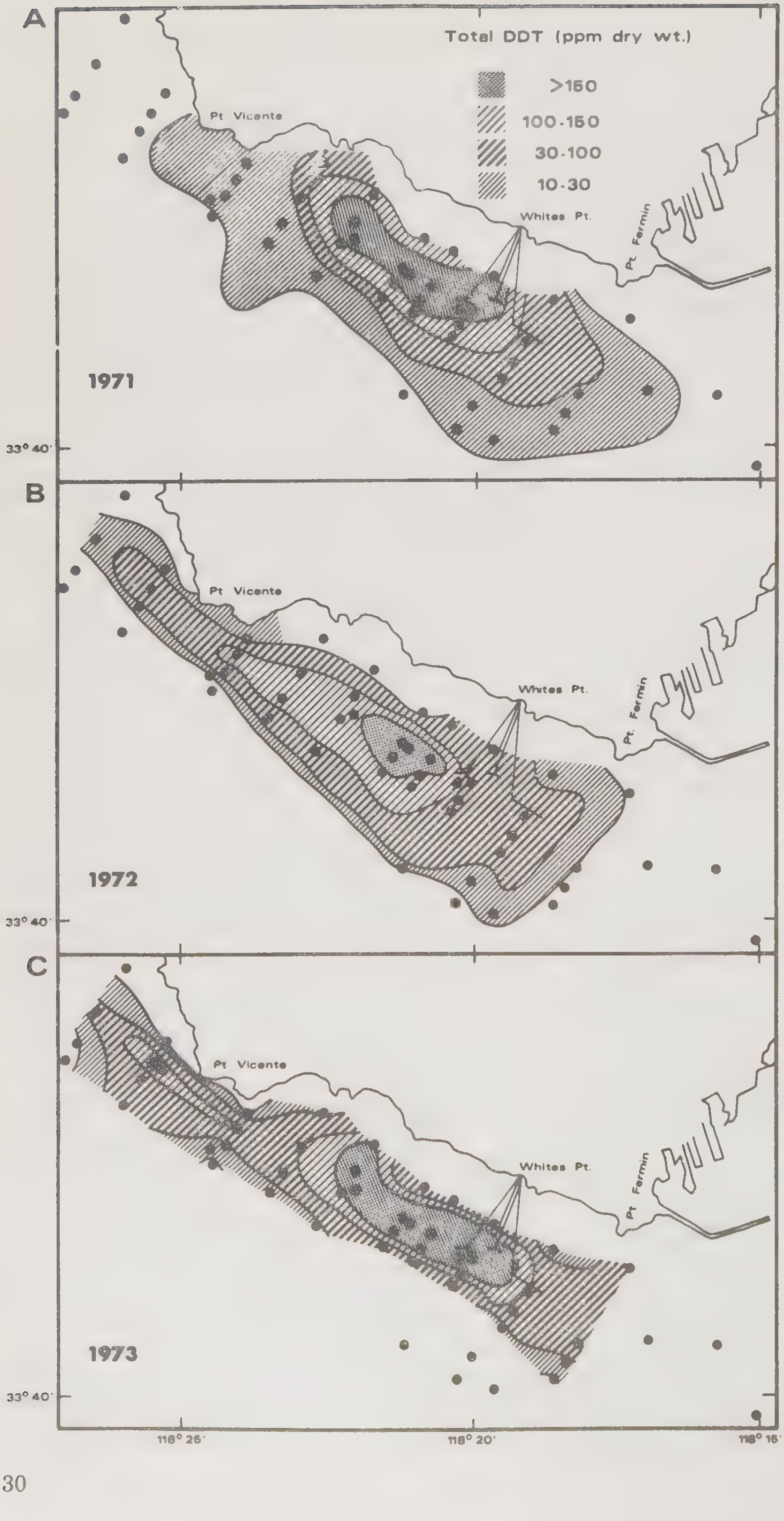

A
Total DDT (ppm dry wt.)
>150
100-150
30-100
10-30
Pt Vicente
Whites Pt.
Pt Fermin
1971
33° 40'
B
Pt Vicente
Whites Pt.
Pt Fermin
1972
33° 40'
C
Pt Vicente
Whites Pt.
Pt Fermin
1973
33° 40'
118° 25'
118° 20'
118° 15'

FIGURE 2.—Total DDT (parts per million dry weight) in the bottom sediments off Palos Verdes in the vicinity of the Los Angeles County sewer outfalls. A. Shipek samples (present paper); B. top 10 cm of gravity cores (McDermott et al. 1974); C. top 5 cm of Shipek samples (McDermott et al. 1974).

depth when the 27 stations of heavy sewer deposition in shallower waters are omitted.

The very high correlation coefficient (0.909) between p,p'DDD/p,p'DDT and p,p'DDE/p,p'DDT shows that when metabolism of DDT to DDD is high, metabolism of DDT to DDE is high also. These high rates of metabolism are negatively correlated with depth. Actually, they are more probably associated with some of the conditions prevailing at depth in the ocean off Los Angeles. The deep areas sampled tend to be anaerobic, and it is probably the lack of oxygen and colder water that determines the low rate of metabolism. The high correlations of the ratios with sample weight and percent water are secondary effects of the correlations of these two factors with depth.

The high negative correlation between p,p'DDE/p,p'DDD and depth indicates that metabolism of DDT to DDE is favored over metabolism to DDD in shallower waters. However, the positive correlation of p,p'DDE/p,p'DDD with p,p'DDD/p,p'DDT (0.297) as well as with p,p'DDE/p,p'DDT (0.446) supports the conclusion that metabolism to both metabolites is much greater in shallow aerobic waters than in deep anaerobic waters. Actually, much more DDT is probably metabolized to DDD than to DDE under all circumstances prevailing in the study area, but the DDE is much more persistent than the DDD and accumulates to a greater degree while DDD is further metabolized to DDMU and other metabolites.

There was at least 10 times as much DDE as DDT in the bottom sediments from stations along the coast of the study area, while 10 stations in deeper waters north of Santa Catalina Island had less DDE than DDT in the bottom samples (Figures 3, 4). DDD tended to follow somewhat the same pattern (Figure 5).

At the 10 stations the average total DDT was 19.9 mg/m², of which 60% was DDT, 19% DDD, and 21% DDE. Mean depth was 341 fathoms (623 m) and the total area represented by the 10 stations was 111 sq nautical miles containing an estimated 5.74 metric tons of total DDT.

It appears that most of the pesticide discharged from the Los Angeles County sewer outfalls has been DDT with the exception of the period of sewer cleaning operations in 1970-71 when DDD and DDE predominated (MacGregor 1974). Most of the DDT settles on the bottom close to the outfalls in shallow waters. Once the DDT becomes part of the bottom sediment it tends to stay there and metabolize in place, rapidly in shallower waters and more slowly in deeper waters.

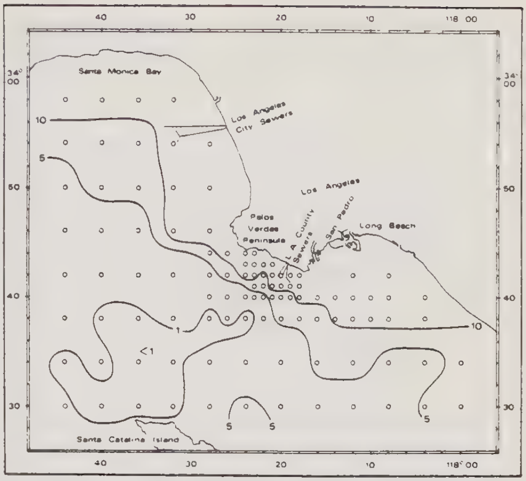


FIGURE 3.—Distribution of ratios of p,p'DDE to p,p'DDT. In the shallow waters near shore the ratios exceed 10:1, while in the deeper waters north of Santa Catalina Island the ratios are less than 1:1.

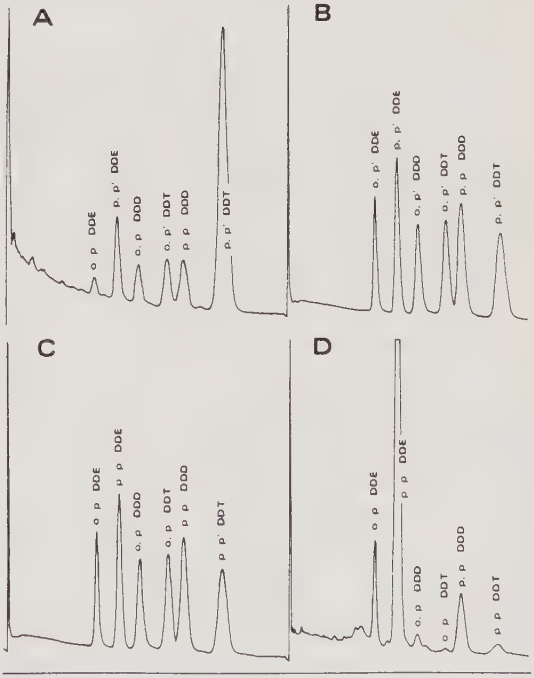


FIGURE 4.—Chromatograms of: A—a deepwater sample (274 m), station 30-40, showing high p,p'DDT peak, and D—a shallow-water sample (36.5 m), station 40-16, showing a high DDE peak. B and C are standards of the DDT analogs.

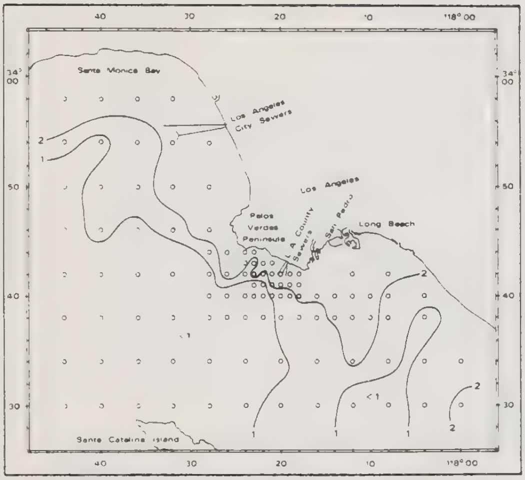


FIGURE 5.—Distribution of ratios of *p,p'*DDD to *p,p'*DDT. In the shallow nearshore areas the ratios exceed 2:1, while in the deeper waters the ratios are less than 1:1. The higher ratios were probably enhanced by sewer cleaning operations in 1970-71.

The DDT deposits in the deeper waters must have been transported there directly from the sewer outlets before much metabolism could take place. If they had originated from bottom sediments closer to the sewer outfalls and in shallower waters, the DDE content would be much higher. DDE averages about 85% of total DDT in biological material in this area; therefore, most of the total DDT in bottom sediments in the deeper water could not have originated from this source.

For the time series for total DDT accumulation in myctophid fish (MacGregor 1974), DDE was less than DDT from 1949 to 1956, but in the subsequent years DDE became much higher. If the deep water with relatively low DDE had resulted from biological fallout as represented by the myctophids for 22 yr (1949-70), and if there had been no metabolism at depth, the DDE would have been twice as high as the DDT rather than one-third as high.

There is either very little metabolism in deep-water sediments, or there is no metabolism, and the small amounts of DDD and DDE found there are the result of fallout from material metabolized in the better-oxygenated surface and intermediate depths.

In commercial DDT, the ratio of *p,p'*DDT to *o,p'*DDT is about 4:1 (i.e., *o,p'*DDT is about 25% of *p,p'*DDT). The distribution of these latter values for the sediment samples indicate that *o,p'*DDT is about what might be expected, while *o,p'*DDD is higher and *o,p'*DDE is lower (Table 2).

In the case of DDT this may mean that *o,p'*DDT metabolizes as readily as *p,p'*DDT. The two high positive correlations with the parameters indicating high metabolism, *p,p'*DDD/*p,p'*DDT and *p,p'*DDE/*p,p'*DDT, may indicate that *o,p'*DDT metabolizes more readily than *p,p'*DDT under conditions of low metabolism of DDT to DDD and DDE. Both the ratios of *o,p'*DDT to *p,p'*DDT and *o,p'*DDD to *p,p'*DDD tend to be high in the bottom sediments north of Santa Catalina Island and in Santa Monica Bay, while ratios tend to be low just south of Palos Verdes Peninsula and in the sandy shallower waters to the east of this area (Figures 6, 7). The association of greater distance from the sewer outfalls and lower total DDT values with high ratios is undoubtedly fortuitous, although the few very high ratios are associated with very low DDT values and probably result from poorer resulting measurements and interfering substances that are no longer completely dominated by DDT at these very low values.

The ratios of *o,p'*DDE to *p,p'*DDE are greater than 1.00:1.00 for 19 stations. Unlike the other two ratios these high ratios are associated with depth. They also tend to be concentrated in the deeper waters just off the Palos Verdes shelf where the sewer outfalls are located (Figure 8). These apparent high relative values of *o,p'*DDE are probably caused by interfering substances, probably DDMU, a metabolite of DDD, which is not being further metabolized under the conditions prevailing at these stations.

TABLE 2.—Frequency distributions of ortho-para isomer as a percent of para-para isomer of DDT, DDD, and DDE in bottom sediments.

Percent	DDT	DDD	DDE
0.0- 5.0	4	0	1
5.1- 10.0	5	0	2
10.1- 15.0	15	0	11
15.1- 20.0	13	7	20
20.1- 25.0	10	8	19
25.1- 30.0	12	16	10
30.1- 35.0	11	24	6
35.1- 40.0	7	16	3
40.1- 45.0	6	9	3
45.1- 50.0	6	9	3
50.1- 55.0	1	1	3
55.1- 60.0	4	4	0
60.1- 65.0	1	1	1
65.1- 70.0	1	0	0
70.1- 75.0	1	1	0
75.1- 80.0	2	0	0
80.1- 85.0	2	0	0
85.1- 90.0	0	0	1
90.1- 95.0	1	1	1
95.1-100.0	0	2	0
>100	1	4	19

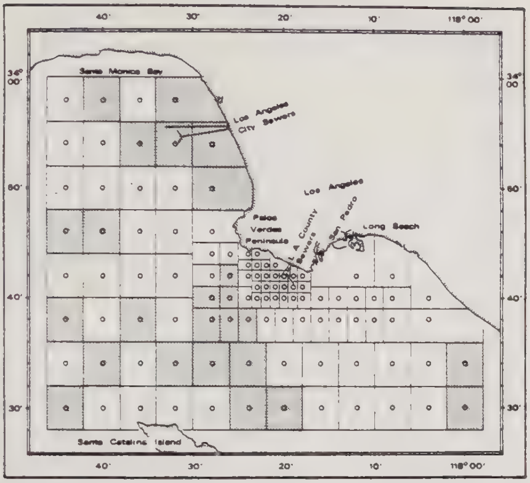
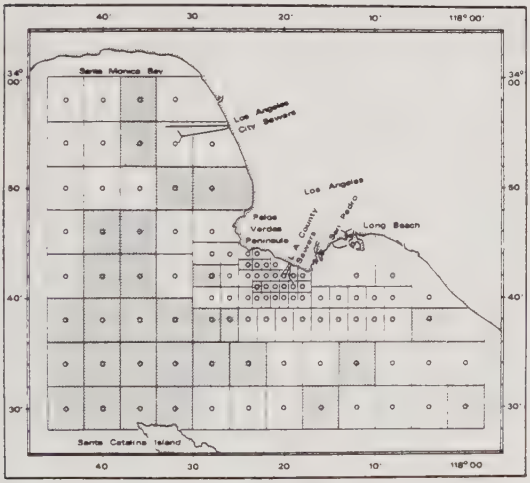

40'
30'
20'
10'
118°00'
34°00'
50'
40'
30'
Santa Monica Bay
Los Angeles City Sewers
Los Angeles
Palos Verdes Peninsula
L.A. County Sewers
San Pedro
Long Beach
Santa Catalina Island

FIGURE 6.—Stations at which the ratio of *o,p'*DDT to *p,p'*DDT was greater than 0.40:1.00.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40'
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Santa Monica Bay
Los Angeles City Sewers
Los Angeles
Palos Verdes Peninsula
L.A. County Sewers
San Pedro
Long Beach
Santa Catalina Island

FIGURE 7.—Stations at which the ratio of *o,p'*DDD to *p,p'*DDD was greater than 0.40:1.00.

To estimate the amount of DDT stored in the bottom sediments in the approximately 911 sq nautical miles between long. 117°58' and 118°46'W and lat. 33°18'N and the California coast, represented by the 103 stations, we must assume that each station is representative of its surrounding area. Each pair of samples from each station showed a high correlation for all pairs of parameters. The correlation coefficient for the logarithms of total DDT for paired samples from 94 stations from which two samples were obtained was 0.964 and the standard error of estimate ±0.321.

The Shipek sampler took bottom silts only to a depth of about 10 cm and sandy bottoms or shallow sediment deposits to a lesser depth. At all stations except those where bottom deposition was very rapid, as near sewer outfalls, all DDT in the sediments was sampled. Near the sewer outfalls the sample represents only DDT deposits in the top 10 cm of sediment. The total amount of DDT determined for the 911 sq nautical mile sampling area was 217 metric tons in the top 10 cm of bottom sediment. Of this total, 179 metric tons (82%) was DDE, 22 metric tons (10%) was DDD, and 16 metric tons (8%) was DDT. McDermott and Heesen (1974) found that the total DDT in the top 5 cm of sediment consisted of 86% DDE, 11% DDD, and 3% DDT in the area of the Palos Verdes shelf. These somewhat different percentages may have resulted from further metabolism of DDT without replenishment. In addition, the DDE percentages tend to be higher in this area, and the DDD was increased in 1970-71 because of sewer cleaning operations.

The total DDT ranged from an estimated 0.42 kg per sq nautical mile at station 30-08 representing 13.3 sq nautical miles to 28.6 metric tons per sq nautical mile at station 43-22 representing 1.25 sq nautical miles.

Five stations representing 6.24 sq nautical miles or 0.7% of the 911 sq nautical mile area represented by the 103 stations contained 47.3%

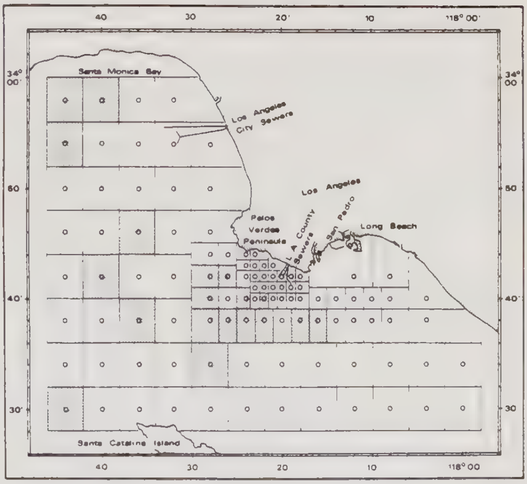
40
30
20'
10
118°00'
34°00'
50
40'
30'
Santa Monica Bay
Los Angeles City Sewers
Los Angeles
Palos Verdes Peninsula
L.A. County Sewers
San Pedro
Long Beach
Santa Catalina Island

FIGURE 8.—Stations at which the ratio of *o,p'*DDE to *p,p'*DDE was greater than 1.00:1.00. The high apparent *o,p'*DDE values probably were caused by DDMU which has the same retention time as *o,p'*DDE on the column used.

of the total DDT (102.7 metric tons). Sixteen stations representing 18.1 sq nautical miles (2.0% of total area) contained 64.0% (193 metric tons) of the total DDT.

Subsamples taken from the tops and bottoms of the blocks of sediment obtained with the Shipek sampler indicated that most of the pesticide was concentrated in the top strata of the samples except for samples taken in the vicinity of the sewer outfalls where deposition was very rapid. Cores were taken from one sample taken near the sewer outfalls and from a second taken at a greater distance from the outfalls to determine more about vertical distribution of DDT in the sediments (Table 3).

At station 42-36 only *p,p'*DDE was measured because DDT and DDD were not readily measurable in the deeper sediment sections. Half of the DDE was found in the top 2 cm, 81% in the top 4 cm, and 95% in the top 6 cm. At station 42-20, close to the sewer outfall where sewer sediment deposition was heavy, there was very little change in the chlorinated hydrocarbon concentrations at all five depths.

Vance McClure (pers. commun.) has provided me with a plot of the depth distribution of DDT, DDE, DDD, and DDMU found in a box core sample taken about 1 nautical mile west-northwest of the sewer outfall. Subsamples were taken from the core at 3-cm intervals from 0 to 12 cm and at 6-cm intervals from 12 to 36 cm. The pesticide values remained high through 12 cm depth and dropped off rapidly between 12 and 18 cm. DDMU had a deeper distribution than the other three components and increased to a maximum at 9 cm and was still present at 36 cm. DDE was last measured at 24 cm, and DDD and DDT at 18 cm. Excluding DDMU, 72% of the pesticide was found in the column corresponding to the top 10 cm and 28% below that depth. Including DDMU, 67% was in the top 10 cm and 33% below.

If the box core sample is typical of the stations near the sewer undergoing rapid sedimentation, about 30% of the pesticide was missed by sampling only to a depth of 10 cm at these stations. Because these stations near the sewer outfalls contain most of the pesticide, the 217 metric tons of pesticide estimated for the entire area in the top 10 cm could be increased to roughly 300 metric tons as a maximum estimate of total DDT in the area.

TABLE 3.—Vertical distribution of DDT in the sediments as determined from core samples taken at stations 42-20 and 42-36.

	Stn. 42-20					Stn. 42-36
Core depth (cm)	*o,p'*DDE (ppm.)	*p,p'*DDE (ppm.)	$\frac{o,p'\text{DDD}}{p,p\ \text{DDD}}$ (ppm.)	$\frac{o,p'\text{DDT}}{p,p'\text{DDT}}$ (ppm.)	Aroclor 1254 (ppm.)	*p,p'*DDE (ppm.)
0-2	14.6	67.4	10.1	3.1	6.2	0.0233
2-4	19.4	90.7	11.4	3.5	6.0	0.0149
4-6	16.2	84.2	10.1	2.9	4.8	0.0063
6-8	34.8	64.4	13.2	3.5	6.2	0.00180
8-10	34.0	79.1	8.2	2.8	4.8	0.00065

In the area of the Palos Verdes shelf only, McDermott and Heesen (1974) estimated that there were 218 tons of total DDT under 62 km^2 of bottom. They calculated that 85% of the total DDT was in the top 12 cm of sediment. If the pesticide is fairly equally distributed in the top 12 cm, about 14% would be in the 10- to 12-cm layer, and the Shipek sampler would sample about 71% of the total DDT.

Sixteen contiguous stations on the Palos Verdes shelf sampled by us in 1971 represented an area of 18.1 sq nautical miles (62.0 km^2) and a total DDT load of 139 metric tons. If this was only 71% of the total DDT in the area (the load of the top 10 cm only), then the corrected estimate including DDT below 10 cm would be 196 metric tons.

McDermott et al. (1974) using a reduced sampling area of 48 km^2 determined that there were 156 tons of total DDT in their revised sampling area. In this present study the area can be adjusted to 48 km^2 by omitting the effect of 2½ peripheral stations. Estimated total DDT then would be 132 metric tons. However, McDermott et al. (1974, table 5) give estimates of total DDT in the area in 2-cm increments down to a depth of 30 cm of sediments. This table indicates that only about 59% of the total DDT is in the top 10 cm in this area. This would increase my estimate of total DDT to 224 metric tons for the 48 km^2 area.

The available data indicate that there is considerable variation in the depth distribution of total DDT in the sediments on the Palos Verdes shelf. However, the general conclusion that can be drawn from the samples is that there are about 200 metric tons of total DDT in the bottom sediments in the 14 sq nautical mile area (48 km^2) in the vicinity of the sewer outfalls and another 100 metric tons in the remaining 897 sq nautical miles of the 1971 survey area.

On 27-28 June 1972, 11 mo after the first samples were taken, additional samples were obtained from seven of the original stations. Four of these stations were in deeper water, between 600 and 890 m deep, and 5 to 11 nautical miles from the sewer outfalls. Total DDT remained low in these stations averaging about 30 mg/m² of bottom, and the composition was essentially unchanged.

The remaining three stations, in areas of much higher pollution within 1.3 nautical miles of the sewer outfalls and in shallower water, showed some apparent changes in grams per square meter of bottom (Table 4).

TABLE 4.—Changes in composition (in grams per square meter of bottom) at stations 42-21, 43-21, and 42-19 in 11 mo.

Station year	Depth (m)	*o,p′*DDE DDMU	*p,p′*DDE	$\frac{o,p'\mathrm{DDD}}{p,p'\mathrm{DDD}}$	$\frac{o,p'\mathrm{DDT}}{p,p'\mathrm{DDT}}$	Total DDT
42-21						
1971	119	0.54	3.45	0.53	0.19	4.71
1972		2.09	3.36	0.61	0.23	6.29
43-21						
1971	33	0.46	1.80	0.33	0.14	2.73
1972		0.99	0.80	0.11	0.05	1.95
42-19						
1971	37	0.38	1.78	0.32	0.14	2.62
1972		0.82	0.71	0.16	0.13	1.82
Totals						
1971		1.38	7.03	1.18	0.47	10.06
1972		3.90	4.87	0.88	0.41	10.06

At station 42-21, DDT, DDD, and *p,p′*DDE remained relatively unchanged with a total of 4.2 g/m² of bottom in both years, while the *o,p′*DDE-DDMU peak increased by almost four times. At the two shallower stations, 43-21 and 42-19, DDT, DDD, and *p,p′*DDE decreased in 1972 to less than half its value in 1971, while the *o,p′*DDE-DDMU peak more than doubled. These changes could be caused by metabolism, by the addition of sewage deposits that were relatively free of DDT combined with metabolism, or even by the removal of a few centimeters of the deposits in the shallow-water areas without metabolism.

CONCLUSIONS

Total DDT in the bottom sediments in the ocean off southern California in an area of 911 sq nautical miles was estimated to be between 200 and 300 metric tons. Most of the total DDT was concentrated in a relatively small area within a few miles of the Los Angeles County sewer outfalls.

Total DDT in the top 10 cm of sediment ranged from 6,600 mg/m² of bottom near the sewer outfalls to about 1 mg/m² of bottom at the more distant stations.

Eighty-two percent of the total DDT was DDE; 10%, DDD; and 8%, DDT. Metabolism of DDT to DDD and DDE was more rapid in shallow waters and apparently very slow or lacking in deep, cold waters that were low in oxygen. Seven samples taken 11 mo later tended to confirm these findings.

ACKNOWLEDGMENTS

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OVARIAN DEVELOPMENT AND FECUNDITY OF FIVE SPECIES OF CALIFORNIA CURRENT FISHES

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ABSTRACT

Four different types of ovarian development in five species of fishes are described. The size distribution of the developing eggs suggests that Pacific herring, *Clupea pallasii,* spawns one batch of eggs during its spawning season; *Vinciguerria lucetia* and Pacific saury, *Cololabis saira,* spawn more than once. The data for jack mackerel, *Trachurus symmetricus,* and Pacific mackerel, *Scomber japonicus,* proved to be inconclusive. The average number of eggs per gram of fish in a spawning batch was *V. Lucetia,* 456; *S. japonicus,* 264; *C. pallasii,* 277; *T. symmetricus,* 109; *C. saira,* 22.

INTRODUCTION

One objective of the California Cooperative Fisheries Investigations (CalCOFI) is to estimate the biomasses of species of California Current fishes from censuses of eggs and larvae of these species. Among data necessary to make such estimates are the number of eggs spawned by the females of each species during the spawning season. This is the product of the number of eggs spawned at each spawning and the number of spawnings per season. Five species of California Current fishes were investigated with respect to types of ovarian development.

The Pacific saury, *Cololabis saira,* is found in the temperate North Pacific from Asia to North America. There is a commercial fishery for saury in the northwestern Pacific, but there is no American fishery. It is important prey species for the albacore, *Thunnus alalunga,* in the North Pacific accounting for 50% or more by volume of the albacore diet (McHugh, 1952; Graham, 1959; Iversen, 1962).

The jack mackerel, *Trachurus symmetricus,* is a commercially important fish in California. The catch reached a peak of 73,000 tons in 1952. Since then this has declined to about 24,000 to 30,000 tons (1968–72). The jack mackerel also is taken from time to time in the sport fishery.

The Pacific mackerel, *Scomber japonicus,* was a commercially important fish in California. In 1935, the catch peaked at 73,000 tons. The catch declined to 600 to 3,500 tons (1965–69), and a moratorium on commercial fishing was declared in 1970. In spite of the decline in commercial catch, the Pacific mackerel has remained an important sport fish for commercial partyboat sports fishermen in southern California.

Vinciguerria lucetia an isospondylid fish of the family Gonostomatidae, is one of the most abundant pelagic fishes taken as larvae in the eastern North Pacific Ocean by CalCOFI. In 1955–57, it was the fourth most abundant fish larva found in CalCOFI net tows. This species accounted for 6.2% of the total larvae taken (Ahlstrom, 1959), ranking only behind northern anchovy, *Engraulis mordax* (33.4%), Pacific hake, *Merluccius productus* (18.5%), and rockfishes, *Sebastes* spp. (7.5%). At the present time no fishery exists for this species.

Unlike the above three groups, *V. lucetia* larvae are more abundant in the southernmost part of the CalCOFI survey area and in the last half of the year, an area and time of reduced coverage by CalCOFI cruises in the three years 1955–57. Ahlstrom and Counts (1958) estimated the number of *V. lucetia* larvae in the CalCOFI survey area between 25° and 37° N latitude at 19.5×10^{12} in 1951, and 19.0×10^{12} in 1952. In addition, *V. lucetia* has a very extensive range outside of the CalCOFI area in the Pacific, Indian, and Atlantic Oceans.

Although it has no direct commercial value, *V. lucetia* is believed to be a significant item in the diets of valuable commercial and game fishes (Ahlstrom and Counts, 1958).

Pacific herring, *Clupea pallasii,* has no commercial or sportsfishing importance in southern California although it is an important commercial species farther to the north. It is included in this study because it illustrates a type of ovarian development different from those of the other four species of fish.

MATERIALS AND METHODS

Fish were obtained from various CalCOFI collections. They were measured and weighed. Gonads were weighed to the nearest milligram and preserved in 3% formalin. Samples of ova were removed from developing ovaries, weighed, and spread with a drop of glycerin on a lined microscope slide. A second slide was lightly taped to the first slide as a cover.

Each slide was projected on a white-surfaced table at a magnification of 50× using a projector designed for scale reading. The diameters of enough yolked ova were measured to determine their size distribution. Additional ova from weighted samples were counted using either the projector or a binocular microscope to obtain an estimate of the number of ova in the ovary.

SPAWNING SEASONS

When the percent spawning by month is averaged over a number of years (Figure 1), we can obtain a general idea of when the spawning will probably occur. But in individual years the spawning is more concentrated in time, and the time of peak spawning may be much later or earlier than indicated by averaged data for several years.

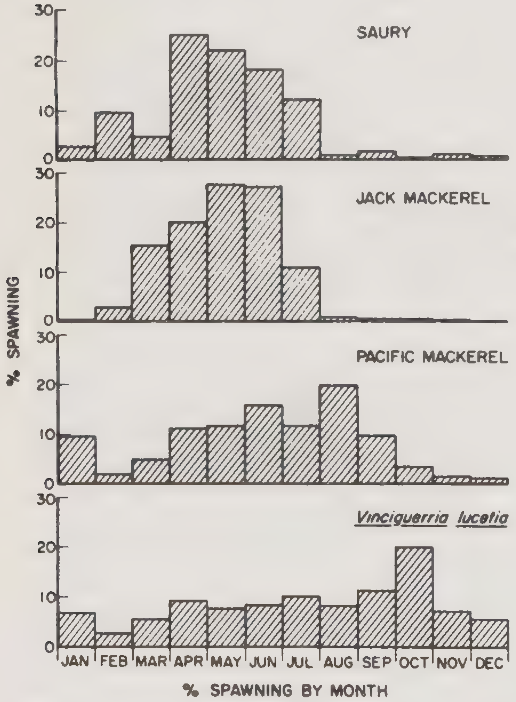

FIGURE 1. Average percent spawning by month. (A) Pacific saury based on standard haul totals of eggs for the years 1950 through 1959. (B) Jack mackerel based on standard haul totals of larvae for the years 1950 through 1959. (C) Pacific mackerel based on standard haul totals of larvae for the years 1951 through 1959. (D) *Vinciguerria lucetia* based on estimates of larval abundance for the years 1951 and 1952.

Pacific Saury

During the decade 1950–59, the 6 month periods of February through July accounted for 91% of the saury spawning (Figure 1A) as indicated by numbers of eggs taken in CalCOFI nets. But, in the individual years, the month of heaviest saury spawning occurred as early as February or as late as July, and an average of 63% of the spawning occurred in the 2 peak spawning months.

Jack Mackerel

Over the same time period, February through July accounted for 99% of the jack mackerel spawning as measured by the presence of larvae in CalCOFI net tows (Figure 1B). The month of heaviest spawning varied from March to as late as July, and an average of 66% of the spawning occurred in the 2 months of heaviest spawning in individual years.

Pacific Mackerel

During the 9 years 1951–59, the 6 months, April through September accounted for 79% of the Pacific mackerel spawning as measured by numbers of larvae taken in CalCOFI nets (Figure 1C). Heaviest spawning occurred as early as January to as late as August. An average of 54% of the spawning occurred in the 2 months of heaviest spawning in individual years.

Vinciguerria lucetia

Based on the numbers of larvae taken in CalCOFI net tows during the 2 years 1951–52, the 6 months May through October, accounted for 65% of *V. lucetia* spawning (Figure 1D). The peak spawning month in both years was October, but only 33% of the spawning took place in the two heaviest spawning months of these 2 years.

V. lucetia and Pacific mackerel have a more southerly distribution than saury and jack mackerel, and they may spawn earlier in the year to the south of the area regularly sampled by CalCOFI.

Pacific Herring

The Pacific herring has a very short spawning season in mid-winter in San Diego Bay, which is the southern limit of its spawning range on the west coast of North America. The demersal eggs of herring are not taken in CalCOFI surveys, but data are included here because these fish illustrate a fourth type of ovarian development.

RESULTS

The two mackerels have similar ovarian development. In immature female fish or in those

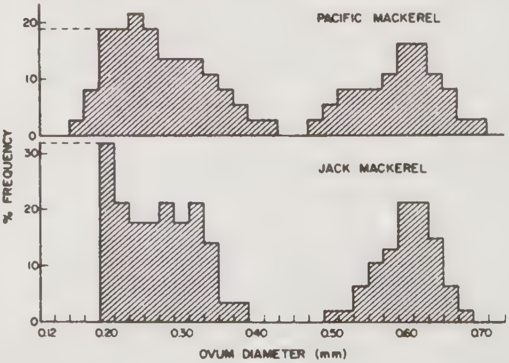

FIGURE 2. Frequency distribution of diameters of yolked eggs in the ovaries of (A) Pacific mackerel, and (B) jack mackerel.

with resting phase ovaries, only transparent eggs less than 0.20 mm in diameter are present. In the earliest stages of development, some of these eggs increase in size and become opaque as yolk material forms within the eggs.

A portion of these yolked eggs continues to grow and eventually forms a second distinct size group (Figure 2). The length of time that the opaque eggs are held at the prespawning stage may be prolonged until external conditions, such as water temperature, are suitable for spawning. Just before the onset of spawning these advanced eggs absorb water, roughly doubling their volume, and become translucent. A perivitelline space is formed enlarging the eggs even more.

Ahlstrom and Ball (1954) state that spawned jack mackerel eggs are 0.90 to 1.08 mm in diameter with a perivitelline space of 0.09 mm and yolk diameters of 0.68 to 0.88 mm (volume 0.16 to 0.26 mm^3). Two jack mackerel in the samples that I examined contained eggs of this size (Table 1).

According to Kramer (1960) freshly spawned Pacific mackerel eggs are 1.06 to 1.14 mm diameter with a perivitelline space of 0.02 mm. Yolk diameters range from 1.02 to 1.10 mm diameter (volume 0.55 to 0.70 mm^3).

The largest eggs (yolk diameters) found in Pacific mackerel ovary samples ranged from 0.57 to 0.77 mm in diameter except for two specimens which contained translucent eggs in the 1.06 to 1.14 mm range. One of these fish appeared to be partly spawned, and the eggs were not counted. The other contained both the large translucent eggs and smaller opaque eggs in the 0.50 to 0.74 mm range. These smaller eggs were found only in the anterior third of the ovary away from the oviduct. An estimate of the opaque eggs in this size group was 130 per gram of fish while the translucent eggs numbered 115 per gram of fish. The total number of eggs per gram of fish was 245, which is lower than the 378 and 319 eggs per gram of fish in the two prespawning females from the same sample. The opaque eggs in the ovaries of this fish were undoubtedly part of the same spawning batch as the translucent eggs but had not yet absorbed water. I have found the same conditions in the ovaries of sardines taken from a school that was actively spawning.

The number of advanced eggs averaged 109 per gram of fish for the 30 jack mackerel examined (Table 1). However, for the 15 smaller fish (217 to 258 mm fork length), the number of eggs was only 66 per gram of fish, while for the 15 larger fish, 438 to 554 mm, it was 152 eggs per gram of fish.

TABLE 1

Fecundity Data for 30 Jack Mackerel, *Thachurus symmetricus*.

Specimen number*	Fork length (mm)	Weight (grams)	Condition factor	Ovary weight (grams)	Gonad index	Advanced eggs		
						Size range (mm)	Number (thousands)	Number per gram of fish
1..........	217	109	106	2.2	2.0	.60–.77	5.1	47
2..........	225	124	109	2.1	1.7	.57–.67	5.2	42
3..........	225	116	102	3.3	2.8	.57–.70	10.3	89
4..........	230	139	114	3.5	2.5	.57–.70	9.9	71
5..........	230	136	112	3.4	2.5	.47–.63	9.9	73
6..........	232	122	98	2.1	1.7	.53–.70	.8	7
7..........	232	132	106	3.1	2.3	.50–.67	7.6	57
8..........	233	139	110	2.8	2.0	.57–.67	3.4	25
9..........	236	139	106	3.8	2.7	.57–.67	8.9	64
10..........	237	135	101	3.5	2.6	.50–.67	7.9	57
11..........	238	167	124	5.6	3.4	.53–.70	20.1	121
12..........	242	168	119	2.4	1.4	.57–.67	1.6	10
13..........	243	154	107	4.8	3.1	.53–.70	18.4	119
14..........	252	178	111	3.8	2.1	.47–.60	13.9	73
15..........	258	200	116	7.4	3.7	.57–.77	26.4	132
16..........	438	907	108	27.6	3.0	.47–.63	94.6	104
17..........	470	1149	111	59.5	5.2	.53–.70	263.	229
18..........	483	1214	104	48.1	4.0	.50–.67	236.	194
19..........	499	1382	111	49.9	3.6	.50–.67	246.	178
20..........	508	1410	108	50.6	3.6	.50–.70	199.	141
21..........	516	1416	103	52.3	3.7	.50–.70	150.	106
22..........	525	1547	107	59.2	3.8	.50–.67	251.	162
23..........	536	1443	94	40.4	2.8	.50–.67	173.	120
24..........	536	1802	117	62.3	3.5	.53–.70	226.	125
25..........	538	1772	114	72.2	4.1	.53–.70	314.	177
26..........	540	1722	109	120.0	7.0	.80–.90	159.	92
27..........	543	1718	107	141.8	8.3	.73–.97	192.	112
28..........	545	1636	101	83.6	5.1	.50–.70	437.	267
29..........	551	1793	107	65.5	3.7	.50–.63	251.	140
30..........	554	1785	105	70.9	4.0	.50–.70	245.	137

* Specimens number 1-15 were taken 95 miles west of San Diego, May 25, 1970, number 16-17, 265 miles west of San Diego, May 7, 1969; number 18-25, 90 miles west southwest of San Diego, June 22, 1970, number 26-30, 6 miles west of San Diego, May 27, 1970. Condition factor equals weight of fish times 10^7 divided by fork length cubed. Gonad index equals gonad weight × 100 divided by fish weight.

TABLE 2

Fecundity data for 18 Pacific Mackerel, *Scomber japonicus.*

Specimen number*	Fork length (mm)	Weight (grams)	Condition factor	Ovary weight (grams)	Gonad index	Advanced eggs		
						Size range (mm)	Number (thousands)	Number per gram of fish
1	273	267	131	6.7	2.5	.44–.60	37.7	141
2	280	358	163	33.3	9.3	.48–.66	163.7	457
3	291	286	116	10.2	3.6	.42–.58	63.1	220
4	314	362	117	21.9	6.0	.48–.70	136.8	378
5	326	375	108	17.0	4.5	.44–.64	119.8	319
6	343	475	118	30.4	6.4	.50–.74	146.6	309
7	328	471	133	35.4	7.5		132.1	281
8	328	493	140	30.7	6.2		127.4	258
9	333	509	138	22.7	4.5	.50–.67	123.7	243
10	335	501	133	26.5	5.3	.60–.73	96.3	192
11	341	545	137	27.0	5.0	.53–.73	104.7	192
12	341	573	145	36.5	6.4	.57–.77	235.0	410
13	342	545	136	36.8	6.8		152.8	280
14	345	541	132	28.0	5.2	.53–.70	116.0	214
15	346	555	134	33.4	6.0		127.4	230
16	350	573	134	23.0	4.0	.53–.67	93.5	163
17	353	602	137	36.0	6.0	.50–.67	181.8	302
18	379	727	134	34.5	4.7		112.6	155

* Specimens number 1–2 were taken in the San Diego area, June 9, 1960, number 3, Hipolito Bay, August 11, 1958; numbers 4–5, San Diego area, June 14, 1957; number 6, Santa Catalina Island, June 5, 1957; number 7–8, 25° 44′ N, 113° 08′ W, January 11, 1970. Condition factor equals weight of fish times 10^7 divided by fork length cubed. Gonad index equals gonad weight × 100 divided by fish weight

The number of advanced eggs averaged 264 per gram of fish for 18 Pacific mackerel (Table 2). There were no apparent changes in the number of eggs per gram of fish over the fork length range of 273 to 379 mm.

During the period of development through spawning, there was no indication of the formation and growth of a second mode of eggs from the mass of smaller yolked and non yolked eggs for either species of mackerel. The ratio of numbers of small yolked eggs to numbers of advanced eggs was 1.5:1.0 for the Pacific mackerel and 1.6:1.0 for the jack mackerel.

The ovaries of immature *V. lucetia* contain only transparent ova less than 0.20 mm diameter. As the ovary develops, a mode of dark yolked eggs is formed (Figure 3A). All of the eggs in this mode continue to grow until they are about 0.48 mm diameter at which time a second mode of dark yolked ova about equal in number to the advanced eggs is formed (Figure 3B, C, D, and E). This secondary mode of opaque eggs is present in fish that contain advanced translucent eggs (Figure 3F, G, and H) but shows little growth until after the advanced eggs have been spawned. This apparent lack of growth in the secondary mode probably results from the very rapid

TABLE 3

Fecundity Data for 16 *Vinciguerria lucetia.*

Specimen number*	Standard length (mm)	Weight (grams)	Condition factor	Ovary weight (grams)	Gonad index	Advanced eggs		
						Size range (mm)	Number	Number per gram of fish
1	34	0.375	95	0.009	2.4	.40–.56	040	107
2	36	0.443	95	0.034	7.7	.52–.66	209	472
3	37	0.475	94	0.014	2.9	.30–.42	177	373
4	38	0.439	80	0.018	4.1	.36–.48	158	360
5	39	0.498	84	0.028	5.6	.54–.70	170	341
6	39	0.521	88	0.014	2.7	.38–.50	157	301
7	40	0.546	85	0.018	3.3	.30–.38	229	419
8	40	0.575	90	0.021	3.7	.38–.46	196	341
9	41	0.602	87	0.021	3.5	.36–.44	189	314
10	42	0.692	93	0.046	6.6	.50–.66	308	445
11	43	0.670	84	0.025	3.7	.22–.36	350	522
12	43	0.693	87	0.037	5.3	.54–.68	191	276
13	44	0.642	75	0.028	4.4	.36–.50	206	321
14	46	0.846	87	0.074	8.7	.54–.70	357	422
15	56	1.448	82	0.086	5.9	.32–.42	1,515	1046
16	56	1.678	96	0.092	5.5	.24–.44	2,064	1230

* Specimens number 1–14 were taken at Guadalupe Island, May 25, 1952, numbers 15–16, 25° 29′ N, 115° 24′ W, August 10, 1953. Condition factor equals weight of fish times 10^7 divided by standard length cubed. Gonad index equals gonad weight × 100 divided by fish weight

growth of the advanced eggs owing to water absorption.

Ahlstrom and Counts (1958) give the diameter of the newly spawned *V. lucetia* egg as 0.58 to 0.74 mm. However, they found that the size of the egg was related to water temperature. Eggs taken in water with a temperature of 16° C averaged 0.72 mm diameter. With increasing temperature, eggs became progressively smaller and averaged only 0.60 mm diameter in water at 28° C.

The 14 specimens of *V. lucetia* taken at Guadalupe Island (29° N lat) ranged in standard length from 34 to 46 mm and averaged 358 advanced eggs per gram of fish (range 107 to 522). The two specimens taken at CalCOFI Station 130.60 (25° 29½′ N lat) were both 56 mm standard length and contained 1,046 and 1,230 eggs per gram of fish (Table 3) or about three times as many eggs per gram of fish as the smaller fish.

Although these two fish were taken farther to the south (and in August) than the 14 fish taken at Guadalupe Island (in May) when the water temperature was undoubtedly higher, the size difference in spawned eggs related to temperature cannot account for the great difference in fecundity. Probably the fecundity increases more rapidly proportionately to weight as the fish grows. This seems to be true also of the jack mackerel.

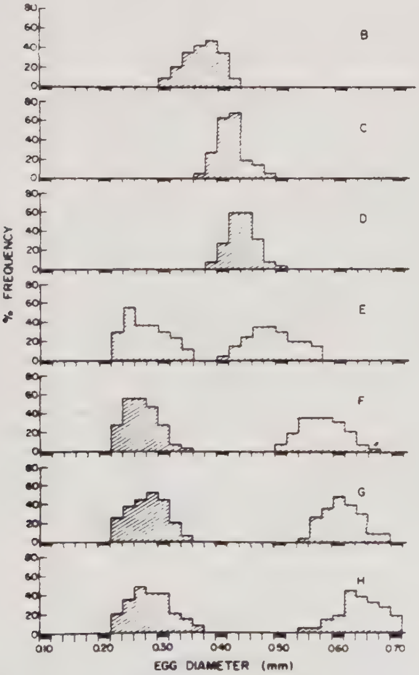

FIGURE 3. Frequency distributions of diameters of yolked eggs in the ovaries of *Vinciguerria lucetia*. (A, B, C, and D) Only the developing mode of yolked eggs (and small nonyolked eggs less than 0.20 mm in diameter) are present during earlier stages of development. (E, F, G, and H) As the advanced eggs develop a second size mode of eggs about equal in number to the advanced mode develops. This second mode of yolked eggs shows little growth as the advanced mode develops to the translucent spawning stage (H).

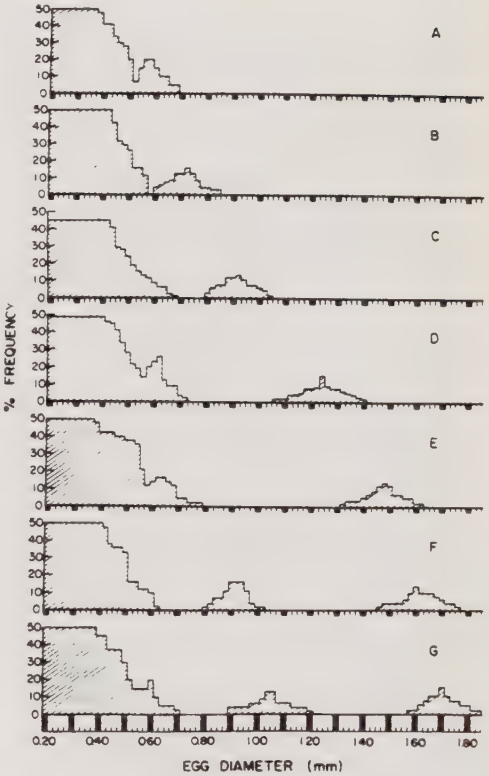

FIGURE 4. Frequency distribution of diameters of yolked eggs in the ovaries of the Pacific saury. At all stages of development a numerous mode of very small yolked eggs is present. (A, B, and C) The smaller group of eggs to be spawned becomes separated from these very small yolked eggs by size during their early development. (D, E) A second mode of eggs about equal in number to the advanced mode begins to develop as the advanced eggs increase in size, and (F, G) becomes completely differentiated by size from the mass of small yolked eggs as the advanced eggs continue to grow and eventually become translucent.

Pacific saury ovaries are elongate and cylindrical. In the immature ovaries of female fish the ova are transparent and less than 0.20 mm diameter. As the fish matures the ova increase in size and darken with yolk formation.

A group of these eggs becomes a distinct size mode and continues to increase in size (Figure 4A, B, and C). As these advanced eggs continue to grow, a second mode becomes distinguishable from the mass

TABLE 4

Fecundity Data for 16 Pacific Sauries, *Cololabis saira*.

Specimen number*	Standard length (mm)	Weight (grams)	Condition factor	Ovary weight (grams)	Gonad index	Advanced eggs		
						Size range (mm)	Number	Number per gram of fish
1	191	27.9	41	0.76	2.7	0.84-1.04	813	29
2	220	46.7	44	2.09	4.5	1.04-1.38	1314	28
3	247	69.9	46	6.63	9.5	1.34-1.74	2188	31
4	252	76.7	48	2.25	2.9	0.82-0.96	1761	23
5	269	88.7	46	6.31	7.1	1.34-1.60	2209	25
6	195	30.4	41	0.96	3.1	1.14-1.64	686	23
7	198	32.3	42	1.13	3.5	1.04-1.42	724	22
8	199	31.6	40	0.59	1.9	0.80-1.04	657	21
9	202	32.0	39	0.88	2.7	0.96-1.26	520	16
10	202	34.3	42	1.38	4.0	1.08-1.38	1016	30
11	203	35.4	42	1.94	5.5	1.48-1.90	(523)**	(15)**
12	207	36.1	41	0.68	1.9	0.76-1.24	542	15
13	208	37.2	41	2.11	5.7	1.56-1.90	(411)**	(11)**
14	184	25.0	40	0.40	1.6	0.82-1.16	225	9
15	215	47.0	47	2.07	4.4	1.58-1.84	(211)**	(4)**
16	281	100.1	45	3.20	3.2	1.50-1.88	1142	11

* Specimen number 1 was taken 100 miles south of San Diego, January 18, 1954; numbers 2-5, off Point Loma, San Diego, February 20, 1950; numbers 6-13; Sebastian Viscaino Bay, March 8, 1954; numbers 14-15, Sebastián Viscaíno Bay, March 8, 1954; number 16, Cortes Bank, October 3, 1949. Condition factor equals weight of fish times 10^7 divided by standard length cubed. Gonad index equals gonad weight × 100 divided by fish weight

** Partly spawned

of smaller opaque eggs (Figure 4D, E). This second mode also becomes a distinct size mode as the first group of eggs approaches maturity (Figure 4F, G). The first mode becomes translucent at 1.50 to 1.90 mm diameter.

When the eggs absorb water and become translucent, they are expelled into the lumen of the cylinder-like ovary. The eggs are held together in a string by sticky filaments at this point. They are spawned in this condition, although the eggs break off into shorter strings during spawning activities.

For 13 Pacific sauries the number of eggs per gram of fish averaged 22 (Table 4; excluding the three fish that were partly spawned). The number of eggs in an advanced mode was approximately equal to the number in a distinct second mode when it was present. The number of small opaque eggs averaged 10 times as many as were in the advanced mode and ranged widely from 3 times to 16 times as many.

Five female Pacific herring taken from San Diego Bay were in prespawning condition. The ovaries of each of these fish contained small transparent eggs less than 0.20 mm diameter and one group of large yolked eggs (Table 5). There were no small or intermediate sized, yolked eggs.

DISCUSSION

Some inferences may be drawn from the size distributions of eggs in the ovaries of fishes. It is generally agreed that the herring spawns only one batch of eggs, and in herring containing advanced eggs, this group is the only group of yolked eggs in the ovary. Observations of spawning and the relatively short spawning season in any one locality tend to confirm this conclusion.

The ovaries of most species of maturing marine fishes, however, appear to contain distributions of egg sizes somewhat similar to those of the two mackerels. There is some controversy among investigators as to whether only the advanced group of yolked eggs or all yolked eggs are spawned during one spawning season.

TABLE 5

Fecundity Data for Five Pacific Herring, *Clupea pallasii*.

Specimen number*	Standard length (mm)	Weight (grams)	Condition factor	Ovary weight (grams)	Gonad index	Advanced eggs		
						Size range (mm)	Number	Number per gram of fish
1	153	53	148	9.27	18.5	1.14-1.36	8,463	160
2	166	75	164	14.65	19.5	1.02-1.24	18,168	242
3	168	67	141	15.97	23.8	1.16-1.38	16,621	248
4	168	84	177	20.15	24.0	1.12-1.30	20,600	245
5	169	87	180	20.96	31.0	1.24-1.50	20,918	240

* Five specimens were taken from San Diego Bay, January 1956. Condition factor equals weight of fish times 10^7 divided by standard length cubed. Gonad index equals gonad weight × 100 divided by fish weight

The most generally held assumption seems to be that because the small eggs do form yolk, they will continue to develop and eventually be spawned as secondary and tertiary spawning batches. But, as the ovarian development of *V. lucetia* demonstrates, a discrete secondary spawning batch of eggs can readily develop directly from the nonyolked oocytes. The lengthy spawning season of this species and the fact that the secondary mode develops during the growth of the advanced mode and approximately equals it in the number of ova present are evidence that *V. lucetia* spawns more than once during the spawning season.

Ovary development of the Pacific saury resembles that of most marine fishes in that a large group of oocytes develop into small, yolked eggs, and from this group a smaller number of eggs continue to increase in size and develop into a spawning batch. The saury differs from most other species in that a discrete secondary batch of eggs about equal in number to the advanced group begins to develop before the advanced group is spawned. Further evidence of multiple spawning in this species is demonstrated in saury #4 (Table 4) which, in addition to the advanced group of eggs 0.82 to 0.96 mm in diameter, contained two large eggs aproximately 1.80 mm in diameter remaining from a previous spawning.

The California grunion, *Leuresthes tennuis,* which spawns on the beaches of southern California and Baja California during the nighttime high tides accompanying the new and full moons is known to be a multiple spawner. This species has a distribution of eggs in the ovaries very similar to that of the saury. In the ovaries of a female grunion (134 mm standard length, 23½ grams) I found 12 large eggs 1.5 to 1.6 mm in diameter remaining from a previous spawning, a discrete group of 1,775 advanced eggs 0.68 to 0.90 mm in diameter, and 5,680 smaller, yolked eggs 0.20 to 0.64 mm in diameter. The larger eggs in this latter group were begining to form a discrete size mode.

Two other atherinids, the topsmelt, *atherinops affinis,* and the jack smelt, *Atherinopsis californiensis,* also have this type of egg distribution in the developing ovaries. Clark (1929) reports finding a few ripe eggs in the lumen of the ovaries of jack smelt that contained developing modes of eggs indicating multiple spawning.

For species of fishes having size distributions of eggs in the ovaries similar to the mackerels, there is no good evidence for multiple spawning. When a few large eggs indicating previous spawning are present in the ovaries, the distribution of small, yolked eggs is much as it is when the advanced mode of eggs is present in the ovaries. No discrete size mode is present indicating that some of the small eggs have developed a new spawning group. Atresia of the smaller eggs is often evident, but until it becomes widespread, the eggs may be classified as developing merely because they contain yolk. The evidence for multiple spawning in species having this kind of ovarian egg size distribution is inconclusive.

SUMMARY

The five species of fishes reported on here illustrate four types of ovarian development. These four types are distinguished by the numbers and size distribution of yolked eggs present in the developing ovaries. The ovaries of all five species contained small transparent eggs containing no yolk material and less than 0.20 mm in diameter.

The prespawning ovaries of the herring contained only these small transparent eggs and the advanced eggs. The prespawning ovaries of *V. lucetia* contained an intermediate mode of developing yolked eggs in addition to the advanced group. The prespawning ovaries of the two mackerels contained a group of small, yolked eggs that is a size continuation of the smaller, nonyolked eggs in addition to the advanced eggs, but there was no intermediate mode of developing eggs. The prespawning ovaries of the Pacific saury contained small, intermediate, and large opaque eggs.

The ratios of small to intermediate to large, yolked eggs for the five species was:

Pacific herring	0.0:0.0:1.0
V. lucetia	0.0:1.0:1.0
Pacific mackerel	1.5:0.0:1.0
jack mackerel	1.6:0.0:1.0
Pacific saury	10.0:1.0:1.0

The data indicate Pacific herring spawn one batch of eggs each season, while Pacific saury and *V. lucetia* spawn more than once. The data for Pacific mackerel and the jack mackerel are inconclusive on this point.

The average number of eggs in the advanced mode per gram of adult female fish was:

Species	Number of fish	Eggs per gram of fish
V. lucetia	16	456
Pacific mackerel	18	264
Pacific herring	5	227
jack mackerel	30	109
Pacific saury	13	22

However, the number of eggs per gram of fish varied considerably. Small fish tended to have much lower relative numbers of eggs than larger fish. This was especially true in *V. lucetia* where 14 small specimens averaged 358 eggs per gram of fish while two large specimens averaged 1,138 eggs per gram of fish, and in the jack mackerel where 15 smaller specimens averaged 66 eggs per gram of fish while 15 larger specimens averaged 152 eggs per gram of fish.

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OCCURRENCE OF THE CARIBBEAN STOMATOPOD, *BATHYSQUILLA MICROPS*, OFF HAWAII, WITH ADDITIONAL RECORDS FOR *B. MICROPS* AND *B. CRASSISPINOSA*

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During the sampling program of the National Marine Fisheries Service (NMFS) aboard the NOAA research vessel Townsend Cromwell in 1972, one specimen of an unusual stomatopod was taken by trawl off Maui, Hawaiian Islands, at a depth of 731–786 m. It proved to be an adult female of the rare *Bathysquilla microps* (Manning, 1961), then known from only three specimens taken in 732–952 m off southeastern Florida and the Bahamas (Manning, 1969a).

Bathysquilla microps was the second species of bathysquillid to be recognized, the first being *B. crassispinosa* (Fukuda, 1909), originally described from Japan and subsequently recorded from additional localities in the western Indian Ocean. It occurs in depths between 230 and 310 m. A third bathysquillid representing another genus, *Indosquilla manihinei* Ingle and Merrett, 1971, was described from a unique specimen taken off Cosmoledo Atoll, Indian Ocean, in a depth of 420 m. Apparently bathysquillids are restricted to moderate depths of the outer shelf and upper slope (Fig. 2).

The bathysquillids live in far greater depths than the majority of known stomatopods. The deepest record given by Kemp (1913) in his monograph of the Indo-West-Pacific stomatopods was 370–419 fm (677–767 m) for *Squilloides leptosquilla* from the "Investigator" collections. Chopra (1939) described

Eurysquilla sewelli from 695 m in the Gulf of Aden and recorded two species from 1295 m in the same area. However, these two species, *Gonodactylus chiragra* (Fabricius) and *Oratosquilla investigatoris* (Lloyd), are known to live in much shallower water (especially *G. chiragra*, an intertidal species), and their occurrence at this depth is questionable. In a review of the western Atlantic stomatopods, Manning (1969a) recorded 14 species from depths greater than 300 m, and only two of these, *B. microps* (732–952 m) and *Squilla intermedia* Bigelow (291–615 m), occurred in depths greater than 450 m.

In reporting this unusual extension of range, we present here additional northwestern Atlantic records for *B. microps*, based on collections made since 1969 by the National Marine Fisheries Service, additional records for *B. crassispinosa*, and comparative diagnoses and sketches for both of these species.

Terms and indices used in the accounts below have been discussed in Manning (1969a). All measurements are in millimeters; total length (TL) is measured on the midline from the anterior margin of the rostral plate to a line between the apices of the submedian teeth of the telson. Station data for the OREGON II collections are on file in the Department of Invertebrate Zoology (Crustacea), National Museum of Natural History, Smithsonian Institution. All specimens are in the Smithsonian.

The illustrations were prepared by Lilly King Manning.

Bathysquilla crassispinosa (Fukuda, 1909)

Figures 1*a–c*, 2

Lysiosquilla crassispinosa Fukuda, 1909:61, pl. 5, fig. 4.

Bathysquilla crassispinosa.—Holthuis, 1967:27 [synonymy to 1967].—Manning 1969a:95, 98.—Holthuis and Manning, 1969:fig. 350–2.—Ingle and Merrett, 1971:197.

Material: Shikoku Island, Tosa Bay, Japan: 1♀ TL (total length) 240 mm.—Madagascar; 18°54′S, 43°55′E; 280–310 m; A. Crosnier, leg.; 24 November 1973: 1♀ TL 215 mm.

Diagnosis: Cornea (Fig. 1*a*) subglobular, fully pigmented, set obliquely on stalk. Rostral plate (Fig. 1*a*) with distinct median longitudinal groove. Antennal protopod with 2 papillae. Dactylus of claw with 9–10 teeth. Carpus of claw with 2 dorsal spines (Fig. 1*b*). Intermediate carinae prominent on thoracic and anterior 2 abdominal somites, unarmed. Third to fifth abdominal somites lacking spinules on posterior

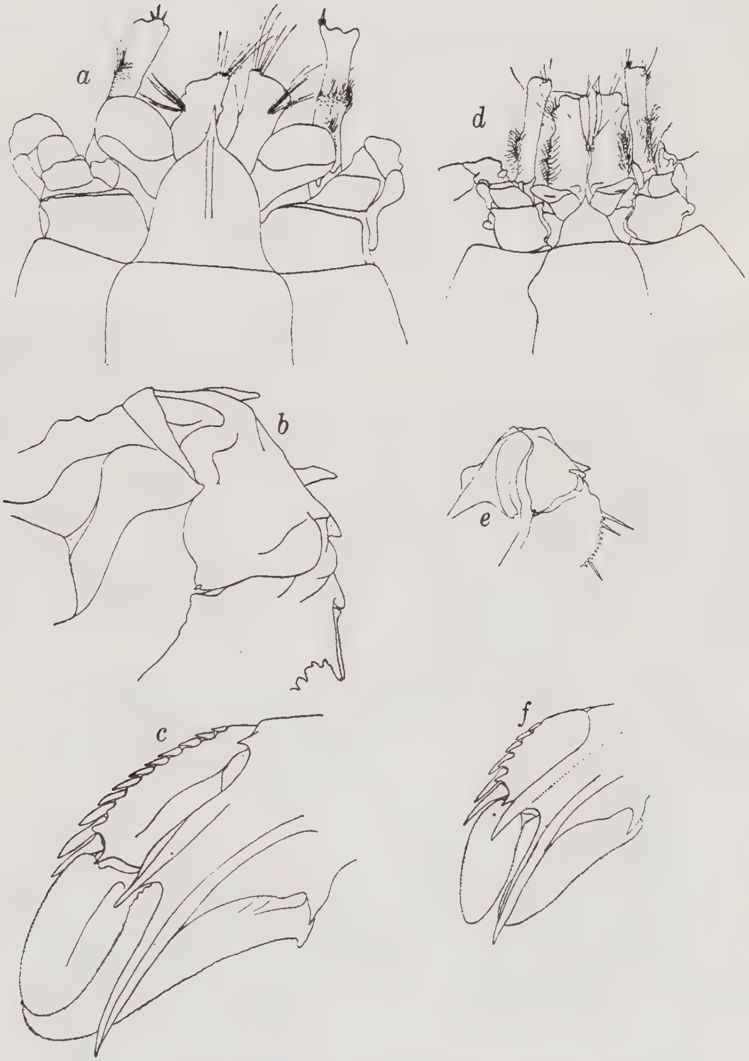

FIG. 1. Front, carpus of claw, and basal prolongation of uropod of: *a–c, Bathysquilla crassispinosa* (Fukuda), female from Madagascar; *d–f, Bathysquilla microps* (Manning), female from Hawaii.

margin. Telson with submedian swellings anteriorly, lacking distinct dorsal submedian carinae. Proximal segment of uropodal exopod with distinct distal spine dorsally, with 10–13 movable spines laterally. Basal segment of uropod (Fig. 1*c*) with spine ventrally at articulation of exopod, endopod with inner basal spine.

Remarks: Although Manning (1969a:95) suggested that the Japanese and South African populations of this species might be distinct, based on discrepancies between published figures, Ingle and Merrett (1971) compared material from the two areas and could find no differences. We observed no differences between our specimens from Japan and Madagascar.

On our specimens of *B. crassispinosa*, the intermediate carinae of the eighth thoracic somite may have a minute, sharp tubercle, but the carinae are not obviously armed posteriorly as in *B. microps*. The posterior segments of the abdomen are more heavily granulated dorsally than in *B. microps*. The merus and propodus of the claw are strongly inflated in large males (TL 285 mm from Tosa Bay, Japan; reported by Ingle and Merrett, 1971), and the strongly curved dactylus has an angular projection as in large males of *Harpiosquilla* (Manning, 1969b), but the antepenultimate tooth of the claw is not reduced as in *B. microps*.

The eyes of *B. crassispinosa*, unlike those of *B. microps* and *I. manihinei*, are relatively large and the cornea is fully pigmented. This must be a reflection of its occurrence in shallower waters than either of the other two bathysquillids.

Komai (1938:270) noted that "the ground color is of the bright orange-red very commonly found in deep-sea crustaceans. The color is especially bright on the exposed thoracic and abdominal somites particularly on the anterior and posterior margins of each somite. The carapace, raptorial limbs and telson are relatively light in color. On the ventral side the pleopods are crimson-red."

Bathysquilla crassispinosa is a large stomatopod, attaining a total length of almost 300 mm; only two other stomatopods, *Lysiosquilla maculata* (Fabricius) and *Harpiosquilla raphidea* (Fabricius), are known to grow to this size. Females of *B. crassispinosa* 200–297 mm long have been recorded in the literature; males appear to be only slightly smaller, with total lengths ranging from 245 to 280 mm.

Our specimens have 2–3 movable and 10–12 fixed propodal spines. The propodal indices are similar to those of *B. microps* 076–078 in two large males examined (TL 250–285 mm) and 070 in a female 215 mm long.

A feature which apparently has escaped notice in the past is the presence, in both species of *Bathysquilla*, of a minute movable tooth at the inferodistal angle of the outer surface of the carpus of the claw (Figs. 1*b*, *e*). So far as we are aware such spines are found in no other stomatopods.

Distribution (Fig. 2): Indo-West-Pacific region, from Japan, the western Indian Ocean, and off South Africa, in depths ranging from 230 to 310 m. Records include JAPAN: Sagami Sea (Fukuda, 1909, 1910); deep part of Sagami Sea (Komai, 1938); off Owase, ca. 300 m (Komai, 1927); Shikoku Island, Tosa Bay (Ingle and Merrett, 1971); Shikoku Island, Tosa Bay, 230–295 m.— MADAGASCAR: 18°54′S, 43°55′ E, 280–310 m.—MOZAMBIQUE: 25°12′S, 34°04′E; 230–295 m (Ingle and Merrett, 1971).—SOUTH AFRICA: Off Natal, north of Durban, 150 fm (275 m) (Calman, 1923; Gordon, 1929; Ingle and Merrett, 1971); off Durban, 29°42′S, 31°29′E, 132 fm (242 m) (von Bonde, 1932; Barnard, 1950; Ingle and Merrett, 1971).

Bathysquilla microps (Manning, 1961)

Figures 1*d–f*, 2

Lysiosquilla microps Manning, 1961:693, fig. 5, pls. 10–11.

Bathysquilla microps.—Holthuis 1967:28 [references].—Manning 1969a: 95, Figs. 26–28.

Material: Gulf of Mexico, Bay of Campeche, Mexico; 700 fm (1281 m); Oregon II Station 10957: 1♂ TL 112.5 mm.—Gulf of Mexico, south of Panama City, Florida; 395 fm (723 m); Oregon II Station 10635: 1♀ TL 175 mm.—North Atlantic, off Surinam; 681–769 m; Oregon II Stations 10604, 10620, 10796: 1♂ TL 187 mm, 2♀ TL 173–220 mm.—Off French Guiana; 604–769 m; Oregon II Stations 10614, 10616, 10803, 10816, 10822: 4♂ TL 176–255 mm, 2♀ TL 183–195 mm.—Pacific Ocean, near Maui, Hawaiian Islands; 21°04′N, 156°09′W; 731–786 m (400–430 fm); 12.5 m shrimp trawl; Townsend Cromwell Station 61–66; 26 October 1972: 1♀ TL 201 mm.

Diagnosis: Cornea (Fig. 1*d*) indistinctly bilobed, set very obliquely on stalk, pigmented part reduced to small, transverse bar. Rostral plate (Fig. 1*d*) not grooved longitudinally. Antennal protopod with 2 papillae. Dactylus of claw with 13–15 teeth (14 in Maui specimen). Carpus of claw (Fig. 1*e*) with 1 dorsal spine. Intermediate carinae of body prominent, armed posteriorly on eighth thoracic and usually on second to sixth abdominal somites, also on first somite in Hawaiian specimen. Third to fifth abdominal somites variously ornamented with spinules on posterior margin. Telson with distinct dorsal submedian carinae. Proximal segment of uropodal exopod unarmed dorsally, with 6–8 (6 only in Maui specimen) movable spines laterally. Basal segment of uropod (Fig. 1*f*) unarmed ventrally at articulation of exopod, endopod unarmed on inner margin.

Remarks: The Hawaiian specimen of *B. microps* agrees in almost all respects with our material from the western Atlantic. The only major difference that we observed was that the Hawaiian specimen has armed intermediate carinae on the first abdominal somite, whereas the intermediate carinae of this somite are unarmed in all of our Atlantic specimens. This single difference in one specimen is not, in our opinion, enough to warrant recognizing a separate Hawaiian subspecies.

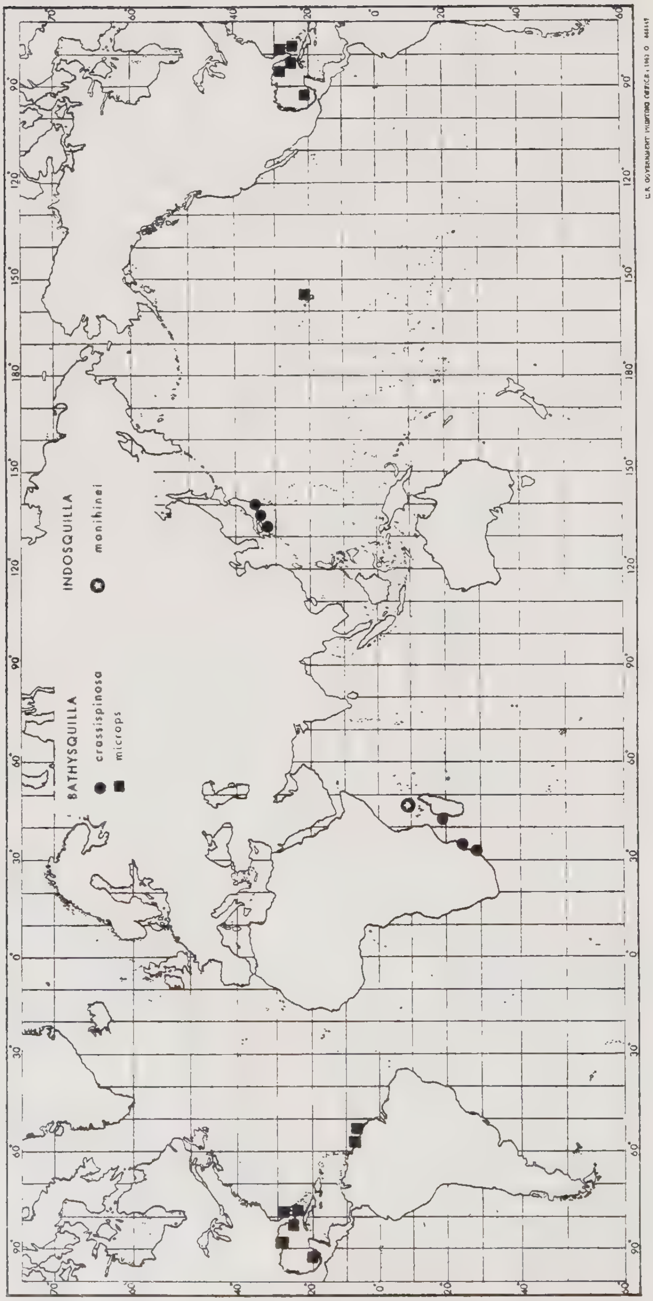
BATHYSQUILLA
● crassispinosa
■ microps
INDOSQUILLA
○ manihinei

FIG. 2. Known distribution of bathysquillids.

The propodal index for five female *B. microps* (TL 173–220 m) ranges from 074–078; it is 074 in the female from Hawaii. Propodal indices of males of *B. microps* from the Atlantic (TL 68–255 mm) range from 074 to 092, the higher indices being found in the smaller specimens. The female from Hawaii has 2–3 proximal movable spines and 12–13 fixed spines on the opposable margin of the propodus of the claw. In Atlantic specimens, there are 2 movable proximal spines and 11–15 fixed spines; of 20 claws examined, 16 were armed with 13–14 teeth. The dactylus of the claw is armed with 13–15 teeth in Atlantic specimens, 14 in the female from Hawaii.

There are 7–8 movable spines on the proximal segment of the uropod in Atlantic specimens, 6 in the female from Hawaii.

Bathysquilla microps may be a slightly smaller species than *B. crassispinosa* which attains a total length of almost 300 mm. Males of *B. microps* have total lengths of 68–255 mm, and females ranging from 44.5 to 220 mm are known.

The color of the female specimen from Hawaii is similar to that of Atlantic specimens, based on photographs by J. E. Randall, Bernice P. Bishop Museum, D. Opresko, University of Miami, and B. Rohr, NMFS. On the Hawaiian specimen the anterior part of the body, from about the level of the antennae and including the eyes, is white; the rostral plate, like the carapace, is pink. The proximal portion of the propodus of the claw is white, the distal portion is pink, and the dactylus is orange. The proximal half of the walking legs is whitish, the distal part is pink. The remainder of the body is pink with orange carinae on the posterior portion of the body. Atlantic specimens show a similar pattern, but specimens have been taken in two color phases, red and orange.

Of the more than 300 shrimp trawl stations effected in the Hawaiian Islands by NMFS during the period 1967–72, the *Bathysquilla* capture occurred at the deepest successful station. Of the total of 300 stations, about 55 were in the 300–800 m depth range. Thus, it would appear that the minimum depth inhabited by *Bathysquilla* in the Hawaiian Island is about 750 m. At this depth the bottom temperature is approximately 5° C. An account of the recent NMFS surveys and the general ichthyological results are given by Struhsaker (1973).

Taxa of fishes associated with the Hawaiian capture of *Bathysquilla* were: sharks (*Apristurus*, *Etmopterus*); the eel families Congridae and Nettastomatidae; Halosauridae; Neoscopelidae; Ogcocephalidae; Ophidioidei; Macrouridae (*Hymenocephalus*, *Malacocephalus*, *Matacocephalus*, *Nezumia*, *Trachonurus*, *Ventrifossa*); Cynoglossidae. The ophidioid fishes represent a species previously recorded only from the western Pacific and the Indian Ocean (Cohen, 1974). Also taken in the haul were three or four species of pandalid shrimps and 25 kg of discarded military ordnance.

During the 1902 expedition to the Hawaiian Islands of the U.S. Fish Commission steamer ALBATROSS, no specimens of *Bathysquilla* were taken. Of the 257 beam trawl stations occupied during that expedition, 88 were in the 700–2800 m depth range. Bigelow (1931) reported on the stomatopods collected during that expedition and recorded only three species which occurred on the upper slope: *Echinosquilla guerinii* (White) in 55–335 m, *Odontodactylus brevirostris* (Miers) in 55–439 m, and *O. hawaiiensis* Manning (as *O. japonicus*) in 110–278 m. Townsley (1953) recorded *E. guerinii* from depths of 92–220 m; all of the other stomatopods reported by Townsley from Hawaii were taken in comparatively shallower water.

Distribution (Fig. 2): Western Atlantic, from localities near Florida, in the Gulf of Mexico, and off northern South America, in depths between 604 and 1281 m, and off Maui, Hawaiian Islands in 731–786 m. Records include: BAHAMAS: Santaren Channel (24°24′N, 80°00′W), 732–860 m (Bullis and Thompson, 1965; Manning, 1969a).—FLORIDA: Off Cape Canaveral (28°03′N, 78°44′W), 915–952 m, and southeast of Tortugas (24°11′N, 83°21.5′W), 732 m (Manning, 1961, 1969a; Bullis and Thompson, 1965); south of Panama City (28°12′N, 86°09′W), 723 m.—MEXICO: Bahía de Campeche (21°31′N, 96°46′W), 1281 m.—SURINAM: 07°49′N, 54°22′W, 732 m; 07°47′N, 54°05′W, 769 m; 07°53′N, 54°04′W, 681–732 m.—FRENCH GUIANA: 07°37′N, 53°32′W, 723 m; 07°35′N, 53°32′W, 604–769 m; 07°32′N, 53°22′W, 641–659 m; 07°18′N, 52°59′W, 668–705 m; 07°06′N, 52°44′W, 668 m.—HAWAII: Off Maui (21°04′N, 156°09′W), 731–786 m.

General Discussion

The discovery of a population in Hawaii of a species previously known from the western Atlantic raises many interesting questions, none of which can be answered with our current state of knowledge. Since bathysquillids represent an old stomatopod stock (see below), it seems likely that the Hawaiian and American populations are relicts of a more widely distributed species, but that the Atlantic populations colonized the Pacific or that the reverse occurred cannot be ruled out. It seems likely that two distinct populations now occur in the two areas, for gene flow between deepwater benthic populations in the western Atlantic and the central Pacific must be minimal, but if genetic differences exist they are not strongly reflected in morphological features. Too, geographically intermediate populations may well exist; the fauna of the upper slope is not that well known in most areas of the world.

Several species or species groups of slope fishes exhibit distributions similar to that of *B. microps*. The macrourid *Hymenocephalus aterrimus* is known only from the tropical western Atlantic and Hawaii in depths of 450–900 m. Marshall and Iwamoto (1973) state that there are virtually no differences between the populations in the two oceans except for a tendency for a slightly greater interorbital width in the Hawaiian specimens. They did not feel that subspecific or other recognition of the populations were required. Iwamoto (1974) recently described a new subgenus and species of macrourid presently known only from the Gulf of Mexico, the Caribbean (732–1062 m), and the Hawaiian Islands (623–705 m). He apparently did not find any morphological differences in the two populations of *Nezumia* (*Kuronezumia*) *bubonis*. This subgenus also comprises a second species which occurs in the South China Sea (Iwamoto, 1974).

The plectognath fish genus *Hollardia* is represented in the tropical western Atlantic by *H. meadi* (Bahamas, Cuba, and Barbados: 135–450 m) and *H. hollardi* (Bermuda, Florida Keys, Gulf of Mexico, Caribbean: 225–915 m). Tyler (1968), in describing *H. goslinei* from Hawaiian waters (365 m), states that it and *H. hollardi* are closely related and have differentiated along the same lines in several important respects, while *H. meadi* differentiated less from the ancestral type, remaining more generalized than the other two species. He also discussed the peculiar distribution of the genus and speculated that the migration of the hollardiins into what is now the tropical western Atlantic must have beeen eastward through the Pacific with *goslinei* being the only presently known Pacific remnant with the extinction of eastern Pacific populations after the reemergence of Central America.

Finally, the Hawaiian endemic bothid flatfish *Chascanopsetta prorigera* was recently reported from the central western Atlantic by Gutherz (1967) on the basis of a still unpublished manuscript. Preliminary comparison of material from the two regions indicates to us that the western Atlantic population deserves recognition as a distinct species. However, these two forms are very close morphologically, and together constitute a distinctive group within the genus.

Such broad distributional patterns are generally rare within the stomatopods. Of approximately 300 species now recognized, only one, *Heterosquilla mccullochae* (Schmitt), can be considered to be pantropical, occurring in the eastern Pacific, the western Atlantic, and the Indo-West-Pacific regions. Five other species occur in both the Atlantic and the Indo-West-Pacific region but not in the eastern Pacific. Broad horizontal distribution patterns also appear to be rare, in general, in inhabitants of the upper slope (Ekman, 1953; Briggs, 1974).

Briggs (1974:435) has pointed out that "many ancient, phylogenetic relicts have accumulated in the slope habitat," and documented this with material recently reported in the literature on a variety of animal groups. The bathysquillids also represent one of these groups, an old stomatopod stock that occurs on the upper slope. The stomatopods are not well represented in the fossil record (Holthuis and Manning, 1969), and there is little evidence to indicate what are old or primitive characters in the group. However, the primary distinction between the single fossil family, Sculdidae, and the four recent families, is the presence of an unsegmented exopod in the sculdids. As Ingle and Merrett (1971) noted, one of the characteristics of *Indosquilla manihinei* is its uropodal exopod, with the distal segment indistinctly sutured rather than distinctly articulated as in all other recent stomatopods. It seems likely that the bathysquillids do represent an ancient stomatopod stock.

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SECOND RECORD OF BLACK SKIPJACK, *EUTHYNNUS LINEATUS*, FROM THE HAWAIIAN ISLANDS

Matsumoto and Kang (1967) reported the first capture of the black skipjack, *Euthynnus lineatus* Kishinouye, in the Hawaiian Islands. Recently (14 July 1975), a second black skipjack was taken in these waters by a Hawaiian pole-and-line skipjack tuna fishing vessel, the *Marlin*, skippered by Walter Asari. The fish was noticed by a fish receiver at Hawaiian Tuna Packers, Richard Howell, who contacted Robert T. B. Iversen, Southwest Region Representative stationed at the Southwest Fisheries Center Honolulu Laboratory. Iversen brought the fish to me for identification.

The specimen, 454 mm fork length, and weighing 1.53 kg, was caught from a school of small skipjack tuna, *Katsuwonus pelamis*, at the extreme tip of Penguin Banks, about 40 km south of the eastern end of Oahu. The specimen is deposited in the U.S. National Museum collection (USNM 214683).

Measurements in millimeters taken according to the methods described by Godsil and Byers (1944) are as follows: Fork length - 454; head length - 126; 1st dorsal insertion - 144; 2d dorsal insertion - 271; anal fin insertion - 306; ventral fin insertion - 144; greatest body depth - 112; greatest body width - 73; dorsal-ventral distance - 108; dorsal-anal distance - 188; ventral insertion to vent - 160; length 1st dorsal base - 130; length 2d dorsal base - 29; length anal base - 25; length pectoral - 70; height 1st dorsal - 61; height 2d dorsal - 28; height anal - 28; diameter of iris - 19; maxillary length - 50; snout to posterior margin of eye - 54.

Counts: 1st dorsal spines - 14, plus 1 imbedded; 2d dorsal rays - 12; dorsal finlets - 8; anal rays - 12; anal finlets - 7; pectoral rays - 26; gill rakers - left side 9 + 1 + 24 = 34, right side 9 + 1 + 25 = 35.

The external characters agree with that of the previous capture (Matsumoto and Kang 1967) and with Godsil's (1954) description of the species. Five black unbranched stripes run parallel to the longitudinal axis of the body on the back from the corselet to the caudal fin, and five or six faint unbranched stripes run horizontally on the belly. Two black thoracic spots are located on each side at the indentation of the corselet near the ventral margin of the body.

The vertebral count is 20 + 17 = 37. As in the previous capture, four large protuberances are present on the 31st vertebra, a characteristic of this species (Godsil 1954).

Although this is only the second specimen recorded, an interview with the skipper of the vessel disclosed that fish similar to this are often caught but are not reported. The question posed in 1967 as to whether this is a chance migrant from the eastern Pacific Ocean still stands.

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Magnitude and ecological implications of thermal inertia in skipjack tuna, Katsuwonus pelamis (Linnaeus)

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Thermal inertia, Tuna, Thermoregulation, Heat Exchanger, Warm Blooded Fish

Synopsis

Heat exchange experiments with sedated and free-swimming skipjack tuna, *Katsuwonus pelamis* (Linnaeus), yielded the following results: For fish between 0.4 and 3.5 kg in weight (W),

1) inertial resistance to cooling and warming were virtually equal over the same span of temperature (18° to 30° C);

2) thermal inertia of red muscle, white muscle, and brain (in intact, living animals) was proportional to $W^{0.45}$ (i.e., coefficient of temperature change, k, $\propto W^{-0.45}$ for each tissue);

3) white muscle, brain, and ventricular blood equilibrated with a changed environmental temperature about 1.1, 3.3, and 20 times as rapidly as red muscle;

4) the countercurrent heat exchanger was about 95% efficient as a thermal barrier between gills and red muscle; consequently, only about half (30%–80%, depending on W) the total heat transfer between the red muscle and the environment occurred across the gills;

5) under conditions of thermal equilibrium, the red muscle and white muscle of sedated fish were warmer than the environment by amounts independent of environmental temperature but proportional to $W^{0.58}$ and $W^{0.61}$, respectively; in contrast, the excess temperature of the brain was independent of fish weight but bore a weak, positive relation to environmental temperature; and,

6) in two free-swimming fish stimulated to violent activity by chasing, the red muscle warmed at rates up to 0.3° C min^{-1}, ultimately attaining temperatures 1.5° and 3.4° C above pre-chasing equilibrium levels.

Comparison of our results with those of other researchers indicated that skipjack tuna exchange core heat with the environment only about 60% as rapidly as do typical teleosts and even somewhat more slowly than do air-breathing aquatic reptiles. Results 1) and 5) were taken to imply no short-term physiological thermoregulation in skipjack tuna; problematic evidence for physiological thermoregulation in other tunas and in aquatic reptiles is discussed. Calculations based on thermal inertia, excess temperature, and rate of warming indicated that minimum and maximum rates of metabolism in the red muscle of skipjack tuna are about 4 and 25 cal g^{-1}hr^{-1}, respectively. Similar considerations suggested that large thermal inertia and high rates of metabolism may pose an ecological problem for skipjack tuna as they grow in body mass: excess core temperatures may become so large that the muscle of the fish overheats, especially during periods of greatest activity in warm waters; speculative upper temperature limits are offered for skipjack tuna as a function of body size and activity level. Two potential benefits of large thermal inertia are discussed and illustrated with simulation models; these are 1) substantial independence from rapid fluctuations of environmental temperature as the fish move between the upper mixed layer and the thermocline, and 2) inertial 'memory' of thermal history to permit or enhance perception of weak temperature gradients.

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* For present address, see p. 80.

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Introduction

A remarkable feature of the tunas (Scombridae) is their tendency to be warmer by several Celsius degrees than the water in which they swim (Barrett & Hester 1964; Carey & Teal 1966 and 1969b; Carey et al. 1971; Stevens & Fry 1971; Linthicum & Carey 1972; and earlier references in Carey & Teal 1966). Such elevated body temperatures are probably unique among teleosts, lamnid sharks (Lamnidae) being the only other group of fishes now characterized as 'warm-bodied' (Carey & Teal 1969a). Both tunas and lamnid sharks are continuously swimming, highly active, pelagic fishes; and, both possess countercurrent heat exchangers in their blood-vascular systems (Carey et al. 1971).

Anatomical descriptions of fishes' heat exchange systems have been provided by Carey & Teal (1969a) for lamnid sharks; by Carey & Teal (1966), by Linthicum & Carey (1972), and by Graham (1975) for tunas of the genus *Thunnus*; by Graham (1973) for the black skipjack, *Euthynnus lineatus* Kishinouye; and, by Stevens, Lam & Kendall (1974) and by Graham (1975) for the skipjack tuna, *Katsuwonus pelamis* (Linnaeus). The essential components of these fishes' heat exchange systems are *retia mirabilia* that retard the transport of blood-borne heat between the gills and core tissues, especially the muscle. Thus, heat generated as a by-product of metabolism is retained, causing elevated temperatures in the muscle mass and nearby tissues. The heat exchanger also damps the influence of changes in water temperature on core temperature. The latter effect has received only a fraction of the attention given to metabolic heat retention, but the two are of course complementary aspects of the same thing—large thermal inertia.

High metabolic rates (Gordon 1968) and large thermal inertia suggest the potential for physiological thermoregulation in tunas. In fact, the work of Carey and his associates (Carey & Teal 1966, 1969b; Carey et al. 1971; Linthicum & Carey 1972; Carey & Lawson 1973) has led to an apparent consensus that at least the larger tunas, such as the bluefin, *Thunnus thynnus* (Linnaeus), do physiologically thermoregulate over broad ranges of environmental temperature. However, Neill & Stevens (1974) have questioned the certainty of rapid physiological thermoregulation in bluefin tuna on grounds that existing data do not offer evidence of short-term variation (controlled or otherwise) in the magnitude of the bluefin's thermal inertia.

The purpose of this paper is to report the results of first experiments on heat exchange processes in a scombrid and to explore the role of large thermal inertia in tuna ecology. The skipjack tuna, physiologically and behaviorally the best known of the tunas, served both as the experimental animal and as the model for several conjectural probes into the thermal biology of scombrids.

Materials and methods

Source and maintenance of experimental subjects

Skipjack tuna, weighing 0.4 to 3.5 kg, were caught on barbless hooks from Hawaiian waters and transported in 2,500 liter shipboard tanks to the National Marine Fisheries Service's Kewalo Research Facility in Honolulu. There, the fish were transferred into 40,000 to 700,000 liter outdoor tanks open to the sky. Both transport and holding tanks were supplied with flowing seawater at 23° to 25° C; in addition, oxygen was bubbled through the water in the transport tanks.

Once each day, skipjack tuna in the holding tanks were offered as much thawed smelt or anchovies as they would eat; most fish fed vigorously by the fifth day in captivity. Every third or fourth day, each skipjack tuna was fed a multiple vitamin, in tablet form, to supplement its diet.

Nakamura (1972) has provided other details of the capture and transport of live tunas and their maintenance at the Kewalo Research Facility.

Cooling and warming experiments

Skipjack tuna were subjected to abrupt 4° to 6° C increases or decreases of water temperature which were maintained until tissue temperatures stabilized. Temperatures of red muscle, of venous blood, or of red muscle, white muscle, and brain simultaneously, were monitored throughout each experiment. From these records, excess temperatures and coefficients of temperature change were determined for each tissue; these parameters were then related to each other, to fish weight, and to other experimental variables.

Experiments were conducted both with sedated, restrained fish and with non-drugged, free-swimming fish. The two experiments with each of two ee-swimming fish were performed to validate the ore efficient but previously untried procedure volving restrained fish, from which the majority f data was obtained.

rocedure with restrained fish

or each set of experiments, one skipjack tuna as removed from a holding tank either by angling ith a barbless hook or by dipnetting. Within 10 c. of capture, the fish was given a 0.2 to 0.6 ml g^{-1} intramuscular injection of sodium pentoarbital (in aqueous solution, 60 mg ml^{-1}) and turned to the holding tank. When, after 10 to 30 in., the sedative caused deterioration of swiming equilibrium, the fish was dipnetted from the nk and secured in a perfusion trough.

The trough was U-shaped in cross-section and ade from inert plastics. Seawater, for respiration d heat exchange, flowed through a plastic pipe at penetrated the trough's incurrent endplate; st through the plate, the pipe ended in a foamastic mouthpiece about which the fish's jaws ere firmly secured. At the opposite end of the ough, a movable excurrent end-plate was posioned to make the effective length of the trough st exceed that of the fish; an overflow outlet in the current end-plate then was adjusted so that the ough's water level just covered the fish's upper rface. Thus, with proper adjustment of length d water depth, the trough's effective volume was ade to conform with body size of individual fish.

Further accomodation for fish size was achieved y using two troughs of different widths. One, for sh weighing less than 3 kg, was 15 cm wide, giving n overall (fish plus water) operating volume that veraged 7 liters per kg of fish. For larger fish, a ough 22 cm wide was used; its overall operating olume was about 8 liters per kg of fish. At least .5 cm of water separated each fish from the nearest ner surface of its trough.

Gill perfusion rates were also varied to accomoate fish of the two size groups: 6 liters min^{-1} for sh weighing less than 3 kg; 10 liters min^{-1} for rger fish.

In addition to binding the fish's jaws around the erfusion mouthpiece, we also secured the fish with vo 3 cm wide straps of knotless nylon netting mm bar mesh) that passed around the animal's unk, one just posterior to the pectoral fin inserons and the other just anterior to the vent. The nds of each strap passed from an anchor at the trough's bottom, then around the body, crossing over the animal's dorsum to anchor points on opposite sides of the trough's rim. The amount of tension in the straps permitted a pencil to be slipped between strap and fish.

After the fish had been secured in the trough and perfusion flow rate and trough volume had been adjusted, sensors for monitoring temperatures of gill-perfusion water, red muscle, white muscle, and brain were placed. Each sensor was a thermistor mounted in the tip of a hypodermic needle, 18 gauge, except 20 gauge for brain. The tip of the water-temperature probe was located in the gill-perfusion flow, just upstream from the incurrent end-plate of the trough. Muscle temperatures were monitored in the region of maximum fish girth. The red-muscle probe was inserted vertically into the deep red muscle, 1 to 2 cm lateral to the 12th or 13th vertebra. White-muscle temperatures were measured in the epaxial mass, at a point in the longitudinal plane 45° above the vertebral-frontal plane and half way between the 14th vertebra and the overlying skin surface. The brain probe was pushed through the pineal window, between the optic lobes, and to a point in or near the diencephalon. Each tissue-temperature probe was securely positioned by first pushing the needle through a 4 mm thick, 20 mm square of Neoprene[1] glued to a 20 mm wide strap of Velcro that passed snugly around the fish's body.

The thermistors were electrically connected to separate channels of an electronic thermometer. Temperature measurements were accurate to 0.1° C, with an operating time constant of about 5 seconds.

Experiments began with each tissue at thermal equilibrium with the perfusion water. Then, the perfusion temperature was abruptly increased or decreased by 4° to 6° C. When all tissues had equilibrated with the new perfusion temperature, the experiment ended. With 8 of the 15 subjects, a second experiment was then performed; this experiment usually involved a perfusion-temperature change opposite in direction but equal in magnitude to that of the first. With four subjects, a third experiment replicated the temperature treatment applied in the first experiment. All experiments were performed within the perfusion-temperature range, 18.3°–29.4° C.

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[1] Reference to trade names does not inply endorsement by the National Marine Fisheries Service, NOAA.

After conclusion of the last experiment in the sequences described above, other experiments were performed on some subjects. In a pair of such experiments with each of three skipjack tuna, we monitored venuous blood temperature as the perfusion water temperature first was increased abruptly from 19° to 23.5° C and then, after the blood equilibrated at 23.5° C, was decreased to 19° C. Each subject began the first experiment of the pair at equilibrium with 19° C water. The probe that had been used to monitor brain temperature was removed, the fish was turned on its side, and the tip of the probe was inserted through the gular isthmus into the bulbus arteriosus of the heart. The fish remained on its side, with the probe tip in the bulbus arteriosus, until both experiments of the pair had been completed.

Procedure with free-swimming fish

For each of two sets of experiments, one skipjack tuna was removed from a holding tank by angling with a barbless hook. The fish was then quickly transferred, in a polyethylene bag with a few liters of seawater, to an experimental tank. The experimental tank was made of fiberglass-reinforced polyester resin, circular in shape with a diameter of 2.4 m, and filled to a depth of 0.6 m with circulating seawater at 24° C.

One or three days later, the fish was caught from the experimental tank and provided with a transducer of red-muscle temperature. The temperature sensor was a thermistor sealed in the tip of a 3 cm long barbed dart made of 12 gauge stainless steel tubing. To implant the sensor, we held the fish by its lower jaw while a stream of 24° C seawater irrigated the gills; the dart was inserted to approximately the same location in the red muscle as that monitored in restrained fish. A 2 mm diameter cord of braided nylon was drawn with a needle (in the manner of a spaghetti tag) through the dorsal white musculature just posterior to the dart's insertion; the ends of the cord then were united above the fish's dorsal midline and connected by another length of cord to a swivel 1.5 m above the tank's water surface. Electrical leads from the thermistor were slackly taped to the cord, from fish to overhead swivel; this arrangement prevented undue strain on the sensor. A mercury-ring connector in the swivel afforded a continuous electrical circuit between the thermistor and the electronic thermometer, despite the circular path the fish would swim upon its release.

Installation of the sensor and related harnessing required 1.5 min. in one case and 2.5 min. in the other; when these were completed, the fish was released into a second experimental tank. This tank was immediately adjacent to the first and identical to it, except 5° C cooler. A lever, on which the swivel had been mounted, was positioned so that the swivel was above the center of the second tank; length of the line between fish and swivel was sufficient to allow the fish access to all parts of the tank.

Activity of the fish, red-muscle temperature, and water temperature were monitored until muscle temperature reached equilibrium. Then a warming experiment was performed. The fish was carefully dipnetted from the 19° C tank and put back into the 24° C tank; simultaneously, the swivel-lever was swung into position above the 24° C tank. Again, fish activity, red-muscle temperature, and water temperature were observed until muscle temperature stabilized.

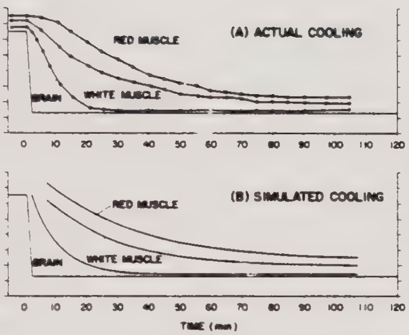
When the warming experiment was completed, the fish was vigorously chased with a dipnet for several minutes to determine the effect of heightened activity on red-muscle temperature. Afterwards, the fish was removed from the tank, weighed, and measured for fork length.

Estimation of heat-exchange parameters

Time series of tissue and water temperatures comprised the primary data from experiments both with restrained and free-swimming fish. From graphical plots of these series (Fig. 1A), an excess temperature and a coefficient of temperature change were estimated for each tissue.

Excess temperature (Stevens & Fry 1970; Neill & Stevens 1974), T_x, was estimated by the difference between tissue and water temperatures at thermal equilibrium. Thermal equilibrium was defined by lack of tissue-temperature change exceeding 0.1° C in a period of at least 10 min. for muscle and brain or 1 min. for blood.

To quantify the rate of each tissue's approach to thermal equilibrium, we calculated the coefficient of temperature change, *k*. The rate of tissue-temperature change was assumed to be directly proportional to the difference between equilibrium and actual tissue temperatures (Neill & Stevens



g. *1.* Actual (A) and simulated (B) time series of tissue mperatures in a 1.60 kg skipjack tuna subjected to an abrupt :crease in water temperature, from 23.5° to 18.3° C. Parameters estimated from the actual series and used in the nulations were as follows:

ssue	*T_x(°C)*	*k(°C min^{-1}°C^{-1})*
ed muscle	1.0	0.034
'hite muscle	0.6	0.043
rain	0.1	0.117

974), the former being a constant function of 'ater temperature and, therefore, itself constant ithin experiments:

$$\frac{\mathrm{l}T_b}{dt} = k[T_e - T_b(t)] \qquad (1)$$

ır, integrating with respect to *t*,

$$\frac{T_e - T_b(t)}{T_e - T_b(o)} = e^{-kt} \qquad (2)$$

vhich gives, after transforming and rearranging,

$$(= -\frac{1}{t}\log_e \left[\frac{T_e - T_b(t)}{T_e - T_b(o)}\right] \qquad (3)$$

vhere k = coefficient of temperature change, °C nin.$^{-1}$°C^{-1}; $T_b(o)$ = tissue temperature, °C, at some initial time; $T_b(t)$ = tissue temperature, °C, ! minutes after the initial time; T_e = equilibrium :issue temperature, °C; and t = time, min., for tissue temperature to change from $T_b(o)$ to $T_b(t)$.

In experiments with restrained fish, $T_b(o)$ for nuscle was taken 5 min. after the perfusion water reached the temperature to be maintained for the duration of the experiment. The 5 min. delay assured complete flushing of the trough by water at the new perfusion temperature and still permitted calculation of *k*'s to be based on temperature differences [i.e., $T_e - T_b(t)$; $T_e - T_b(o)$] at least an order of magnitude larger than experimental noise (±0.1° C). Brain and venous blood changed temperature more rapidly than muscle, making it necessary to take $T_b(o)$ for these tissues as soon as the perfusion temperature reached its experimental level. Complete flushing of the entire trough was not as critical for accurate estimation of brain and blood *k*'s as for muscle *k*'s. The brain exchanged heat primarily with water in the incurrent one-third of the trough, throughout which part flushing was complete within 30 sec. Heat exchange between blood and water occurred primarily at the gills, where water temperature lagged perfusion temperature changes by less than 5 sec.

To maximize comparability of data from restrained and free-swimming fish, we took $T_b(o)$ for red muscle in free-swimming fish at 5 min. after the fish was put into the experimental tank.

After $T_b(o)$ and T_e had been read from a given time-series plot, *k* was then calculated from equation (3) by finding $T_b(t)$ at $t = \lambda$ such that $[T_e - T_b(t)]/[T_e - T_b(o)]$ was 0.37:

$$k = -\frac{1}{\lambda}\log_e(0.37) \simeq \frac{1}{\lambda}. \qquad (4)$$

Evaluation of heat-transfer pathways: gills versus outer body surface

To assess the relative contribution of gills versus outer body surface to heat exchange in skipjack tuna, we estimated for red muscle, white muscle, and brain the proportion of total heat transfer via the gills. These data were collected from each of seven restrained fish immediately after it had served in the cooling/warming experiments described above.

The gills and mouth of each fish were perfused with seawater different in temperature from that which bathed the general skin surface. This was accomplished by maintaining the usual gill-perfusion flow at 28° to 29° C (variation less than 0.2° C within experiments) while water at 23.5 ± 0.1° C flowed directly into the incurrent end of the trough at 30 liters $min.^{-1}$. Mixture of the two flows provided a bath surrounding the fish that varied less than 0.2° C throughout the trough and was about 4° C cooler than water perfusing the gills. Dual-temperature perfusion continued until tissue temperatures equilibrated.

The proportion of heat transferred via the gills was estimated by considering for each tissue the measured equilibrium temperature relative to the equilibrium temperatures that hypothetically would have obtained had the entire fish been bathed in water at either gill-perfusion temperature or at trough temperature:

$$T_e = \alpha(T_{ag} + T_x) + (1 - \alpha)(T_{ab} + T_x) \qquad (5)$$

which gives, after rearranging and simplifying,

$$\alpha = \frac{T_e - T_{ab} - T_x}{T_{ag} - T_{ab}} \qquad (6)$$

where α = proportion of heat transferred via gills (and mouth); T_e = measured equilibrium temperature, °C; T_{ag} = gill-perfusion temperature, °C; T_{ab} = trough temperature, °C; and, T_x = excess temperature, °C, measured in preceding series of cooling/warming experiments.

Results

Activity and behavioral responsiveness of fish (steady state)

Even sedated fish exhibited swimming activity and were responsive to touch throughout the major part of each experimental set. Characteristically, violent bursts of activity gave way to strong, rhythmic swimming at 2 to 4 tail beats $sec.^{-1}$ after fish had been in the trough 10 to 30 min. Thereafter, both the amplitude and frequency of tail beats gradually decreased until, after a few hours, swimming motions generally were weak or ceased entirely. Occasionally, tail beating resumed or became stronger for periods lasting up to an hour during the course of an experimental set. Throughout all experiments reported in this paper, fish that had become immobile still 'gasped' in response to a finger's touch on the opercular margin.

Free-swimming skipjack tuna swam continuously at 1.5 to 3 body lengths $sec.^{-1}$, with 2 to 4 tail beats $sec.^{-1}$, except during the terminal experiments in which they were chased. Chasing caused fish to swim at speeds in excess of 10 body lengths $sec.^{-1}$, decreasing to 5 body lengths $sec.^{-1}$ as the fish tired. Only brief (less than 5 min.) increases in swimming speed followed transfer between experimental tanks.

Neither restrained nor free-swimming fish varied activity in a way detectably related to temperature.

Excess tissue temperatures (steady state)

Excess temperatures ranged from 2.6° C in the red muscle of one free-swimming and one restrained fish to 0.0° C in the brain of several restrained fish.

For restrained fish, potential dependence of red muscle, white muscle, and brain excess temperatures on several independent variables was evaluated by step-wise linear regression analysis (Dixon 1967). The following full model was assumed:

$$\log T'_x = \beta_0 + \beta_1 \log W + \beta_2 T_a + \beta_3 t + \beta_4 d + \epsilon \qquad (7)$$

where $T'_x = \left| \begin{array}{l} T_x, \text{°C, for red and white muscle;} \\ T_x + 1, \text{°C, for brain;} \end{array} \right.$ W = fish weight, kg; T_a = perfusion temperature, °C; t = time, min., in the trough; d = sedative dosage, ml kg^{-1}; β_i = regression parameters; and, ϵ = random experimental error. The analysis yielded the following set of reduced regression equations [$P \leq 0.05$; $(a \pm b)_{95\%}$ indicates 95% parametric confidence interval on a]: for red muscle,

$$\begin{aligned} \log T_x = {} & 0.1608 + (0.5800 \pm 0.3350)_{95\%} \log W \\ & - (0.0009 \pm 0.0006)_{95\%}\, t, \\ & R = 0.62^{**}\ (n = 26); \end{aligned} \qquad (8)$$

for white muscle,

$$\begin{aligned} \log T_x = {} & 0.1110 + (0.6067 \pm 0.3883)_{95\%} \log W \\ & - (0.0009 \pm 0.0008)_{95\%}\, t, \\ & R = 0.57^{*}\ (n = 25);\ \text{and} \end{aligned} \qquad (9)$$

for brain,

$$\begin{aligned} \log (T_x + 1) = {} & -0.1724 \\ & + (0.0105 \pm 0.0045)_{95\%}\, T_a, \\ & R = 0.69^{**}\ (n = 26). \end{aligned} \qquad (10)$$

Thus, excess temperature relations of red and white muscle were similar to each other but markedly different from that of brain. Sedative dosage alone among the independent variables failed to affect significantly excess temperature of any issue among the three.

Variation in fish weight and time in the trough ignificantly affected excess temperatures of both red and white muscle. Excess temperatures of the wo muscle tissues differed only in their means; both responded, with almost identical slopes, posi-ively to increases in fish weight and negatively to ncreases in trough-time. For a given fish weight and rough-time, excess white muscle temperature was about half the corresponding excess red muscle temperature; consideration of paired red and white muscle T_x's (Fig. 2) confirmed this result. Point solutions of equations 8 and 9 for T_x at $t = 300$ min. ($\simeq \bar{t}$) are 0.46° and 1.61° C for red muscle, and 0.24° and 0.89° C for white muscle of restrained fish weighing 0.4 and 3.5 kg, respectively.

Two observations were made on excess red muscle temperature of each free-swimming skipjack tuna; these were 1.2° and 1.5° C for the 1.21 kg fish, and 1.7° and 2.6° C for the 1.78 kg fish. Solving equation 8 for point estimates of T_x at $t = 0$ min. gives 1.62° and 2.02° C for restrained skipjack tuna weighing 1.21 and 1.78 kg, respectively.

In contrast to muscle, brain excess temperature depended only on perfusion temperature; increase in brain T_x was associated with increase in T_a. Point solutions of equation 10 for T_x are 0.04° C for minimum T_a, 18° C, and 0.39° C for maximum T_a, 30° C.

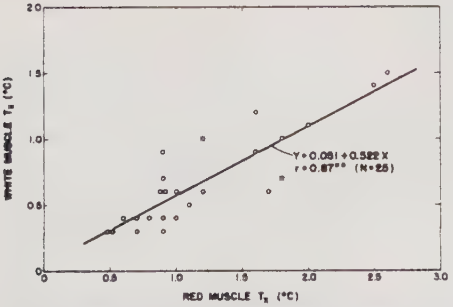


Fig. 2. Relation between excess temperatures of red and white muscle in skipjack tuna. Each point indicates one of 25 paired observations; data were collected from 15 sedated fish.

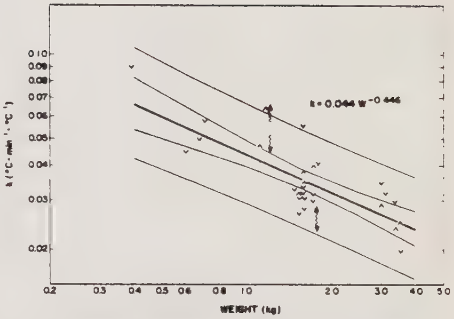


Fig. 3. Relation between fish weight and the coefficient of temperature change (k) in the red muscle of skipjack tuna. Point symbols indicate values determined by cooling restrained fish (v), by warming restrained fish (Λ), by cooling free-swimming fish (⧫), and by warming free-swimming fish (⧫). The heavy middle line is the regression of k on weight for both cooling and warming experiments with restrained fish: the inner and outer pairs of lighter lines indicate 95% confidence intervals (about the regression line) for expected k given weight and for a single observation on k given weight, respectively.

Excess temperatures of venous blood were too small to be reliably measured when the entire fish was at thermal equilibrium. However, the relatively slow rate of temperature change in the muscle mass permitted indirect estimation of blood excess temperatures from the ratio, $(T_a - T_{bl})/(T_a - T_{rm})$, where T_{bl} was blood temperature when its rate of change just slowed to approximate the rate of change in non-equilibrium red muscle temperature, T_{rm}. Values of the ratio from two experiments with each of three skipjack tuna (weighing 1.55 to 1.61 kg) ranged from 0.075 to 0.285 with a median of 0.11. This implies that excess temperature of venous blood was about 11% of the corresponding red muscle T_x.

Coefficients of tissue-temperature change

Red muscle, white muscle, and brain of restrained skipjack tuna cooled and warmed at rates inversely proportional to fish weight (Figs. 3–5). Double logarithmic plots of the coefficient of temperature change, k, against fish weight appeared linear, with slopes for all three tissues identically equal −0.45 to two decimal places. Red and white muscle yielded k versus W relations not only alike in slope

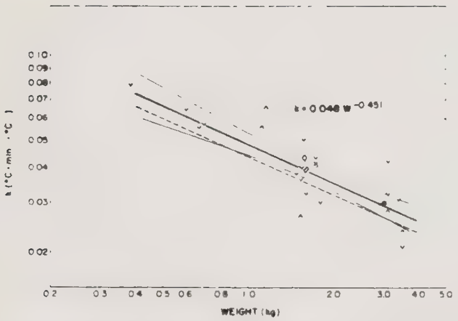


Fig. 4 Relation between fish weight and the coefficient of temperature change (k) in the white muscle of skipjack tuna. Point symbols indicate values determined by cooling (v) and warming (∧) restrained fish. The heavy solid line is the regression of k on weight for both cooling and warming experiments; the pair of lighter solid lines indicates the 95% confidence interval (about the regression line) for expected k given weight. The dashed line gives the regression of red muscle k on weight (from Fig. 3) for comparison.

but also in mean ($P \leq 0.05$; Fig. 5). Brain cooled and warmed about 3.3 times as rapidly as muscle of the same fish, over the fish-weight range 0.4 to 3.5 kg. For fish weighing 1.6 kg, at least, venous blood changed temperature about 20 times faster than muscle (Fig. 5).

The above relations were developed without distinction between warming and cooling experiments, because we found no evidence for a systematic difference between warming and cooling k's. Both warming and cooling k's were available from each of seven restrained skipjack tuna ranging in weight between 1.55 and 3.53 kg. Geometric means of the quotient, warming k/cooling k, were 1.07, 0.99, and 0.96 for red muscle, white muscle, and brain, respectively. For each tissue, the quotient 1.0 fell well within the 95% parametric confidence interval on the geometric mean. Thus, none of the tissues warmed at a rate significantly different from the rate at which it cooled.

Red muscle k's from free-swimming fish were similar to those obtained from restrained fish. One free-swimming fish yielded k's larger, and the other k's that were smaller than those of similarly-sized restrained fish. Only one of the four values from free-swimming fish fell outside the 95% parametric confidence interval on red muscle k, given weight, for restrained fish (Fig. 3).

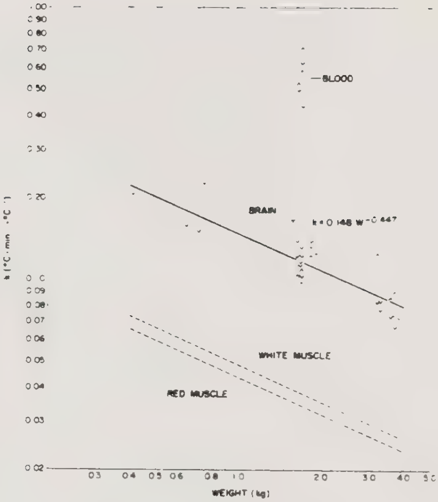


Fig. 5. Relation between fish weight and the coefficients of temperature change (k) in the brain and venous blood of skipjack tuna. Point symbols indicate values determined by cooling (v) and warming (∧) restrained fish. The heavy solid line is the regression of brain k on weight for both cooling and warming experiments; the pair of lighter solid lines indicates the 95% confidence interval (about the regression line) for expected brain k given weight. The dashed lines give the regressions of red and white muscle k on weight (from Figs. 3 and 4) for comparison.

Red muscle temperatures of highly active (chased) fish

Red muscle temperatures of free-swimming skipjack tuna increased from their equilibrium values at rates of about 0.3° C min.$^{-1}$ during the first few minutes of chasing (Fig. 6). Maximum temperature attained by red muscle of the larger fish was 29.6° C – 3.4° C over the equilibrium temperature and 5.7° C greater than water temperature. This temperature was reached after 15 min. of chasing, when the fish stopped swimming and lost attitudinal equilibrium; the fish did not resume swimming and had no detectable heart beat 15 min. after chasing ended. The smaller fish was chased 4.5 min. until the onset of exhaustion became evident. After an 18.5 min. 'rest' period, chasing was resumed for 2 min.; the fish then stopped swim-

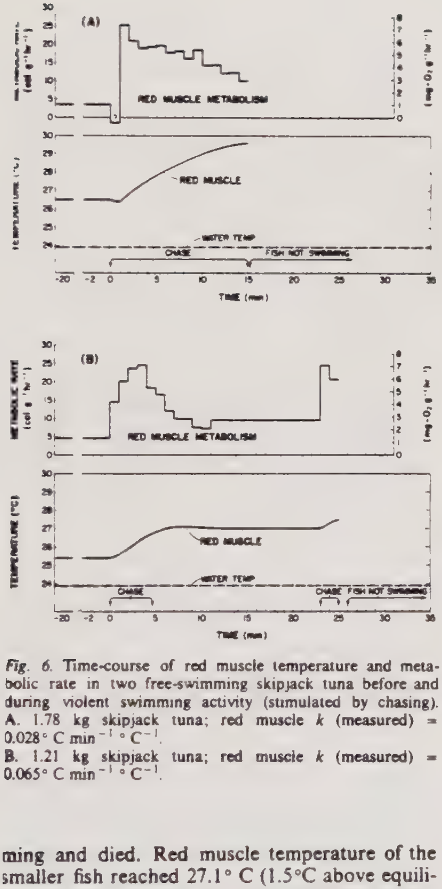


Fig. 6. Time-course of red muscle temperature and metabolic rate in two free-swimming skipjack tuna before and during violent swimming activity (stimulated by chasing). A. 1.78 kg skipjack tuna; red muscle k (measured) = 0.028° C min^{-1} ° C^{-1}.
B. 1.21 kg skipjack tuna; red muscle k (measured) = 0.065° C min^{-1} ° C^{-1}.

ming and died. Red muscle temperature of the smaller fish reached 27.1° C (1.5°C above equilibrium temperature and 3.2° C above water temperature) shortly after the first period of chasing ended, remained almost constant at 27.0° C during the rest period, and had increased to 27.5° C when swimming stopped following the resumption of chasing.

Proportion of heat transfer via gills

The gills accounted for a larger fraction of heat transfer between the environment and red muscle

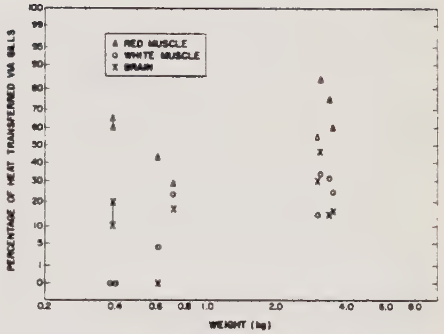


Fig. 7. Relation between skipjack tuna weight and the fraction of heat transfer accomplished by way of the gills. Two replicate observations (symbols connected by a line) were made for each tissue in the 0.4 kg fish; single observations were made for each tissue in each of the other six fish.

than between the environment and white muscle or brain (Fig. 7). Deep, well vascularized red muscle effected 27% to 84% of its heat exchange via the gills. Percentages of gill heat-transfer were similar for white muscle and brain, ranging from 0% to 35% and from 0% to 46%, respectively.

A part of the inter-fish variation in gill heat-transfer seemed to be associated with variation in fish size. Red muscle, white muscle, and brain of larger skipjack tuna tended to exchange more heat via the gills than did respective tissues of smaller skipjack tuna (Fig. 7).

Discussion

Adequacy of exponential model for rates of tissue-temperature change

We, like other students of heat exchange in aquatic poikilotherms (Bartholomew & Lasiewski 1965; Stevens & Fry 1970; Weathers & White 1971; Spray & May 1972), adopted an exponential model to describe rates of temperature change. The basic model has been called 'Newton's law of cooling' (Kleiber 1972, among many others) and, more appropriately, 'Newton's law of excess temperature' (Fry 1967). In conformity with the reasoning of Neill & Stevens (1974), we used T_e instead of the more conventional value, T_a, in equation 1 and in its descendants.

Temperature change in one tissue of skipjack tuna could not have been wholly independent of simultaneous temperature changes in other tissues. The effective driving gradient of temperature at each anatomical point was the difference, $T_e - T_b$. Although T_a was constant, T_e must have continuously changed as temperatures of surrounding tissues changed and as (if) metabolism at the point varied. Therefore, the model specified by equation 1 could not have been strictly appropriate, because absolute constancy in T_e was not achieved.

Despite weakness of the model on theoretical grounds, we accepted it as adequately descriptive of the process of concurrent temperature change in the various tissues of living skipjack tuna. Grounds for the model's acceptance included the lack of significant differences between *k*'s determined by cooling and warming experiments and the close agreement between actual cooling/warming curves and those simulated by application of equation 2 with empirically derived parameters (e.g., Fig. 1, cf. panels A and B).

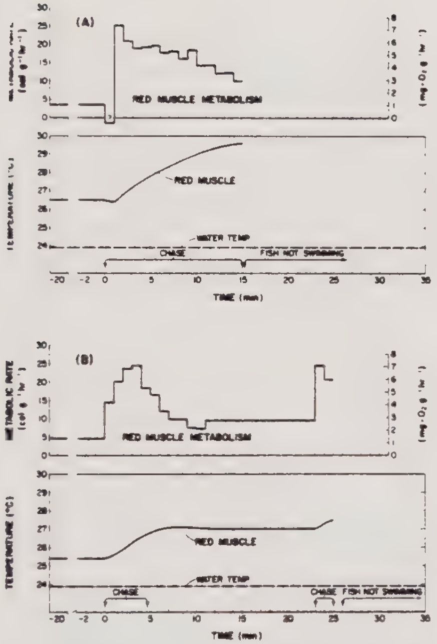
Physiological thermoregulation in skipjack tuna and other aquatic poikilotherms

Countercurrent heat exchangers in the circulatory systems of tunas (Carey & Teal 1966; Linthicum & Carey 1972; Graham 1973, 1975; Stevens, Lam & Kendall 1974) and lamnid sharks (Carey & Teal 1969a) provide these fishes with one essential ingredient of physiological thermoregulation — large thermal inertia that retards the loss of metabolic heat, resulting in large excess body temperatures. However, realization of physiological thermoregulation must also involve a second essential ingredient, the ability to *control* excess body temperature so that it varies inversely with environmental temperature. Such control could be achieved either by decreasing metabolic rate or, more logically, by increasing *k* as environmental temperature increases.

Large bluefin tuna, *Thunnus thynnus* (Linnaeus), and shortfin mako, *Isurus oxyrinchus* Rafinesque, have smaller excess body temperatures when caught in warm waters than when they are taken in cold waters (tuna: Carey & Teal 1969b; Linthicum & Carey 1972; shark: Cary & Teal 1969a). Thus, these fishes would appear to be capable of considerable physiological thermoregulation, at least when exposure to a given environmental temperature persists for the days or weeks necessary for acclimatory adjustments. On the basis of telemetry experiments, Carey and his associates (Carey et al. 1971; Carey 1973; Carey & Lawson 1973) have carried the case for physiological thermoregulation in the bluefin tuna further by suggesting that large bluefin are capable of rapid physiological thermoregulation in the same sense as mammals. Neill & Stevens (1974) have offered a different interpretation of these telemetry data — i.e., that the observed responses of body temperature to changes in water temperature could simply reflect constant but small *k* coupled with constant heat production to produce a constant T_x (large thermal inertia, but no physiological thermoregulation).

Our warming and cooling experiments yielded no evidence for physiological thermoregulation in skipjack tuna. Excess temperatures of red and white muscle were statistically unrelated to environmental temperature. Brain excess temperatures not only were small but also varied directly with environmental temperature (presumably an Arrhenius effect), whereas physiological thermoregulation requires an inverse relationship between T_x and T_a. Moreover, there was no indication that tissue *k*'s varied systematically with either the level of T_a or direction of change in T_b. Therefore, our experiments offer no support to the hypothesis of Stevens & Fry (1971) that '. . . skipjack tuna [physiologically] regulate their body temperature over an ambient temperature range of about 25°–34° C.'

Many investigators of reptilian thermobiology (Bartholomew & Tucker 1963, 1964; Bartholomew & Lasiewski 1965; Bartholomew, Tucker & Lee 1965; Weathers & White 1971; Spray & May 1972) have construed dissimilar rates of warming and cooling to indicate physiological thermoregulation. In fact, several circulatory mechanisms whereby reptilian *k*'s may change in response to temperature have now been demonstrated (Heath, Gasdorf & Northcutt 1967; Baker & White 1970; Weathers & White 1971). However, the fact that reported rates of warming exceed those of cooling for the majority of lizards and turtles (see compilation of data by Spray & May 1972) may be attributed in part to the convention of calculating rates of temperature change as if dT_b/dt were a linear function of $T_a - T_b$. Neill & Stevens (1974) have argued that such cannot be the case for animals that maintain excess body temperatures. Whenever $T_x > 0$ ($T_e - T_a > 0$), $|T_a - T_b|$ will exceed



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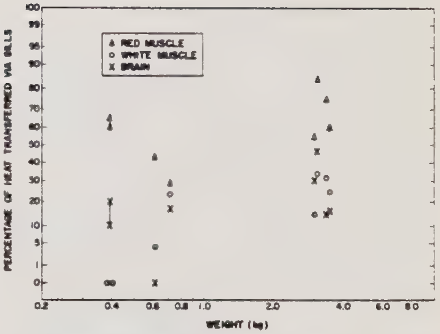

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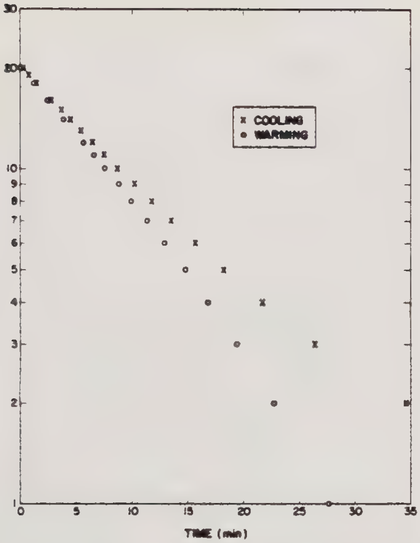


g. 8. Simulation of cooling and warming curves for a point the body of an aquatic poikilotherm that has constant = 1.0° C and constant k = 0.0856° C min^{-1} °C^{-1} (for both oling and warming). |ΔT| is the absolute difference between dy temperature and water temperature. Note that the curves e, in fact, curves rather than straight lines and that the te of cooling is less than that of warming even though the s are identical.

$T_e - T_b|$ when the animal is cooling and will be ess than $|T_e - T_b|$ when the animal is warming given the same $|T_a - T_b|$ and T_x in the two experinents); this relation leads automatically to the esult that $d|T_a - T_b|/dt$ is greater for warming han for cooling when *k* is the same for warming nd cooling (Fig. 8). (For terrestrial poikilotherms nder conditions of low relative humidity, T_x may e negative owing to evaporative cooling [e.g., Whitfield & Livezey 1973]; then, $d|T_a - T_b|/dt$ is reater for cooling than for warming, given contant *k*.) Moreover, *k*'s calculated from the relaion

$$k' = -\frac{1}{t}\log_e\left[\frac{T_a - T_b(t)}{T_a - T_b(o)}\right] \qquad (11)$$

re in error by an amount that increases as $T_b(t) - T_a$ approaches T_x; i.e., 'k' approaches zero as $T_b(t) - T_a$ approaches T_x (because *t* approaches ∞).

Bartholomew & Tucker (1963), recognizing the flaw inherent in calculations of *k* based on $d|T_a - T_b|/dt$, corrected their apparent *k*'s for the effects of metabolism; heart rate was monitored in bearded dragon, *Amphibolurus barbatus*, undergoing temperature change and then indexed to equivalent heat production according to heart-rate/O_2 consumption relations determined from separate experiments at constant temperatures. Spray & Belkin (1972) have since pointed out that heart rate in *Iguana iguana* is linearly related to temperature of blood flowing through the heart, which, in iguana (Spray & Belkin 1973) as in skipjack tuna, has less thermal inertia than the body 'core.' Thus, heart rate in a lizard or fish whose body temperature is changing would appear a poor indicator of metabolic heat production.

Spray & May (1972) used oxygen consumption data from the literature to correct their apparent *k*'s for several turtles. They concluded that resting metabolism alone was not enough to account for differences between observed heating and cooling rates, suggesting that turtles are capable of changing *k* by altering blood flow to the periphery of the body in response to changes in temperature.

Rates of heat exchange in skipjack tuna and other aquatic poikilotherms compared

Stevens & Fry (1974) have compiled coefficients of core-temperature change for fishes and aquatic reptiles. Comparing cores of animals with equal weight, our skipjack tuna equilibrated with a new water temperature only about 60% as rapidly as typical teleosts (Catostomidae) and even somewhat more slowly than aquatic reptiles (turtles of the genera *Pseudemys* and *Chelydra*, and the Galápagos marine iguana, *Amblyrhynchus cristatus*). Considering that fishes must achieve respiratory exchange with water (which has much greater heat capacity and much less oxygen per unit volume than air), the observation that skipjack tuna exchange heat more slowly than aquatic lung-breathers is evidence of high efficiency in the skipjack's countercurrent heat exchanger.

Red muscle, white muscle, and brain of skipjack tuna—despite marked differences in vascularization and distance from the skin surface—yielded *k*'s related to body weight by almost identical exponents of weight: −0.446, −0.451, and −0.447. We know of no other published study in which rates of temperature change were monitored simultaneously at several locations within a fish. Spray & Belkin (1973) observed that the cloaca and head of terrestrial lizards have greater thermal inertia than the heart and lungs, but these authors presented no information on the relation between thermal lag of lizard tissues and body weight.

It seems to us that k's measured very near the skin surface ought to be weight-independent ($\propto W^0$), whereas the relation between core k and body weight should be similar to that between the inverse of mean blood circulation time (between tissue and heat sink/source) and body weight. That weight exponents for red muscle, white muscle, and brain k's of skipjack tuna were virtually identical, non-zero values suggests that the heat exchange process of overwhelming predominance in all three tissues was convection, especially forced convection via blood circulation.

Efficiency of skipjack tuna heat exchanger as a thermal barrier

Present data permit coarse estimation of the efficiency with which the countercurrent heat exchanger of skipjack tuna acts as a thermal barrier. The estimate is provided by considering the median temperature excess — 0.11 times that of red muscle — carried by venous blood just before it reached the gills (T_{xbl}). Calculation of efficiency is based on the following estimates and assumptions:

1) Of venous blood in the bulbus arteriosus, 60% has passed through the countercurrent heat exchanger and 40% has not (Stevens, Lam & Kendall 1974).

2) Arterial blood entering the heat exchanger has no temperature excess.

3) Venous blood entering the heat exchanger has a temperature excess equal that of red muscle (T_{xrm}).

4) Venous blood not passing through the heat exchanger has a temperature excess (T_{xvo}) equal that of the body average excluding red muscle; we assume $T_{xvo} \simeq 0.2\ T_{xrm}$.

5) Changes of blood temperature in the veins are negligibly small.

6) Venous blood from all tissues has mixed thoroughly by the time it reaches the bulbus arteriosus.

If all the above statements are correct, then the temperature excess of venous blood leaving the heat exchanger (T_{xvhe}) may be calculated as follows:

$$0.6\ T_{xvhe} + 0.4\ T_{xvo} \simeq T_{xbl}; \quad (12)$$

$$0.6\ T_{xvhe} + 0.4\ (0.2\ T_{xrm}) \simeq 0.11\ T_{xrm}; \quad (13)$$

thus,

$$T_{xvhe} \simeq 0.05\ T_{xrm}. \quad (14)$$

This calculation implies that the heat exchanger's efficiency as a thermal barrier is about 95%.

Another way of examining thermal efficiency of the skipjack tuna's heat exchanger is by comparison, with non-scombrid teleosts, of the gill's relative importance as an avenue of heat transfer. Unfortunately, relative contributions of gills and other pathways to core heat exchange are not empirically known for typical fishes (Stevens & Fry 1970). However, the predominant opinion among fish physiologists seems to be that expressed by Fry (1967, p. 308): '. . . the overwhelming fraction of heat transfer [in typical gill-breathers] probably takes place at the respiratory surface. . . .' Thus, typical fishes weighing 0.5 kg may achieve 95% of core heat transfer via the gills as opposed to only 50% in skipjack tuna of the same weight. If resistance to heat exchange by other routes is the same in the two types of fishes, the difference between the above percentages suggests that the heat exchanger of skipjack tuna provides at least 20 times the resistance of typical teleosts to core heat transfer via the gills.

Excess tissue temperatures of skipjack tuna

For a fish to have tissue temperatures much different from ambient temperature, one or both of two circumstances must obtain: (1) the fish encounters rapidly changing environmental temperatures and is not, therefore, continuously in equilibrium with environmental temperature, or (2) the fish has a high metabolic rate and large thermal inertia. Large thermal inertia is important in (1) as well as in (2), in that the time required to reach thermal equilibrium depends directly on thermal inertia.

Both circumstances apply in the case of tunas. The magnitude and cause of tunas' large thermal inertia have been discussed above. It remains to develop the evidence that tunas voluntarily subject themselves to rapid changes of environmental temerature and that tunas have unusually high metaolic rates.

Yuen (1967)[2] used CTFM sonar to observe hort-term vertical movements of tuna schools in Iawaiian waters. Skipjack tuna, observed while ley fed at the surface, moved vertically at speeds p to 3.3 m sec^{-1} and sounded to depths of 195 m; irface and 195 m temperatures were 26.4° and 6.2° C, respectively. Skipjack tuna and kawaawa, *Euthynnus affinis* (Cantor), have been obrved visually from a submarine at depths as reat as 150 m, where water temperature was 7.8° C (Strasburg, Jones & Iversen 1968). We ave trained captive skipjack tuna to swim repeatdly between connected tanks whose temperatures ere 24° and 18° C, respectively.

Metabolism of free-swimming skipjack tuna eighing 0.4 to 3 kg is minimally 0.5–0.6 mg $)_2\ g^{-1}\ hr^{-1}$ and exceeds 2 mg $O_2\ g^{-1}\ hr^{-1}$ under onditions of moderate swimming activity (R. M. Booding and W. H. Neill, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Ionolulu, HI 96812, unpublished data). These alues are 3 to 5 times larger than those for noncombrid teleosts of similar size (cf. Brett 1972). tevens (1972) has pointed out several features of irculatory and respiratory physiology that corelate with the skipjack tuna's high metabolic rate; .g., the effectiveness with which skipjack remove xygen from water is 90%, a value 3 to 9 times igher than for non-scombrid fishes.

Stevens & Fry (1971) measured excess tissue emperatures of skipjack tuna immediately after apture at sea and after various periods of time in aptivity. One sample of 20 just-caught fish, averagng 1.64 kg in weight, had excess red muscle, white nuscle, and brain temperatures averaging 9.1°, .6°, and 4.5° C, respectively. After 10 days in aptivity, fish from the same school had excess emperatures about one-third those of just-caught ish; 35 more days in captivity resulted in no further lecreases in excess tissue temperatures.

Stevens & Fry (1971), like other workers who lso have measured large excess temperatures in ust-caught skipjack tuna (Barrett & Hester 1964; Carey & Teal 1969b), made their observations on ish that were in a state of 'feeding frenzy' (Strasburg & Yuen 1960) when caught. Neither Stevens & Fry (1971) nor we were able to generate comparable excesses in captive skipjack tuna, even through violent chasing.

We doubt that wild skipjack tuna have excess body temperatures much different from those of equally active captive fish. Moreover, the observation that schools of skipjack tuna are highly variable in the extent to which frenzy feeding develops upon live-bait chumming (Yuen 1959, 1966) suggests that variation in excess red muscle temperature may be as much a function of activity and feeding motivation as of ambient temperature. Stevens & Fry (1971) supposed that relatively small excess red muscle temperatures in skipjack tuna caught from 28° to 30° C waters reflected physiological thermoregulation at ambient temperatures above 25° C.

Heat production by red muscle of skipjack tuna

Gordon (1968) found that unstimulated, minced preparations of red muscle from skipjack tuna metabolize at about 2.1 mg $O_2\ g^{-1}\ hr^{-1}$. Our experiments with intact skipjack tuna yielded data on red muscle metabolism that can be compared with Gordon's (1968) measurements from excised tissue.

To arrive at estimates of red muscle metabolism we reasoned that the rate of heat production, *r*, at a point in the red muscle is proportional to the rate of potential temperature decrease, $k(T_{rm} - T_a)$, plus the rate of any actual change in red muscle temperature, dT_{rm}/dt, given constancy in T_a:

$$r \propto k(T_{rm} - T_a) + dT_{rm}/dt. \qquad (15)$$

Under conditions of thermal equilibrium and constancy in *r*, this proportionality reduces to

$$r \propto k \cdot T_x, \qquad (16)$$

and, finally, to the equations,

$$r(\text{cal } g^{-1}\ \text{min}^{-1}) = 0.8\ k \cdot T_x, \qquad (17)$$

given that the heat capacity of fish muscle is about 0.8 cal $g^{-1}\,°C^{-1}$ (Slavin 1964; Charm & Moody 1966), and

$$r(\text{mg } O_2\ g^{-1}\ hr^{-1}) = \frac{60 \cdot 0.8}{3.42} k \cdot T_x = 14.0 \cdot k \cdot T_x, \qquad (18)$$

Yuen, H. S. H., 1967. Short term vertical movements of skipack tuna. Report presented at 18th Pacific Tuna Conference, ake Arrowhead, November 1967. Report on file Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Ionolulu, HI 96812.

given that the oxycaloric equivalent for fish is about 3.42 cal mg O_2^{-1} (Warren & Davis 1967).

For red muscle of skipjack tuna weighing *W* kg and restrained for *t* min., we estimated that

$$\log k = -1.356 - 0.446 \log W \qquad (19)$$

and

$$\log T_x = 0.161 + 0.580 \log W - 0.0009\, t. \qquad (20)$$

Logarithmically transforming equation 18 and then substituting into it the above relations with t = 0, we have

$$\log r = \log 14.0 + \log k + \log T_x \qquad (21)$$

and

$$\log r(\mathrm{mg\ O_2\ g^{-1}\ hr^{-1}}) = -0.049 + 0.134 \log W. \qquad (22)$$

Solutions of equation 22 at W = 0.4 kg and W = 3.5 kg are 0.79 and 1.06 mg O_2 g^{-1} hr^{-1}, respectively. [We note that equation 22 implies an increasing rate of red muscle metabolism for increasing size of sedated skipjack tuna. In most fishes, whole-body routine metabolic rate decreases as size increases (whole-body rate $\propto W^{-0.2}$; Beamish & Dickie 1967); however, whole-body routine metabolic rate of skipjack tuna appears independent of fish weight, at least over the range 0.3–5.0 kg (R. M. Gooding, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, unpublished data).]

We attribute the difference between Gordon's (1968) and our estimates of metabolic rate in skipjack red muscle primarily to the vast difference between the methods of respirometry *in vitro* and direct calorimetry *in situ*. Gordon (1972, p. 249) has cautioned that his measurements were '. . . from substrate saturated, non-contracting preparations . . . [and, therefore,] give no information as to the properties of active, functioning muscle exposed to physiologically more normal substrate supplies.' Our data, we believe, are the first for any fish to provide the sort of information to which Gordon referred.

Recourse to the basic calorimetric proportionality, together with the constants assumed above, allowed us to estimate heat production rates in the red muscle of two skipjack tuna that were forced to high levels of activity by chasing (Fig. 6). T_{rm} and dT_{rm}/dt were estimated for 1 min. intervals; tank temperature, T_a, was constant. The values of *k* used were those estimated earlier from temperature-change experiments with the same fish and probe placement. Heat production rates prior to chasing were about 4.7 cal g^{-1} hr^{-1} (1.4 mg O_2 g^{-1} hr^{-1}) in the 1.21 kg fish and 3.5 cal g^{-1} hr^{-1} (1.0 mg O_2 g^{-1} hr^{-1}) in the 1.78 kg fish; maximum rates of heat production were about 25 cal g^{-1} hr^{-1} in each fish (Fig. 6). The maximum rates of heat production corresponded to a rate of oxygen demand exceeding 7 mg O_2 g^{-1} hr^{-1}. It is unlikely that such a large demand could be met aerobically (see Brett 1972); the result of continued forced activity, then, was a lethal oxygen debt.

Inferred upper environmental temperature limits for skipjack tuna

Considerations like those of the previous section suggest that large thermal inertia and high rates of metabolism may pose an ecological problem for skipjack tuna as they grow in body mass: excess core temperatures may become so large that the muscle of the fish overheats, especially during periods of greatest activity in warm waters.

Maximum red muscle temperatures observed from skipjack tuna cluster about 35° C (Stevens & Fry 1971). Suppose that the red muscle of this fish cannot function on a sustained basis at temperatures higher than 35° C. (In reality, the limiting upper temperature for red muscle operation may be subject to acclimatory adjustment.) Then, the maximum environmental temperature, max T_a, at which skipjack tuna can live indefinitely is a function of metabolic rate and thermal inertia, the latter depending on body size:

$$\max T_a = 35. - T_x \qquad (23)$$

$$= 35. - \left(\frac{3.42}{60 \cdot 0.8} \cdot \frac{r}{k}\right) \qquad (24)$$

$$= 35. - \frac{0.071\, r}{k}. \qquad (25)$$

From equation 19,

$$k = 0.044 W^{-0.446}. \qquad (26)$$

Therefore,

$$\max T_a = 35. - (1.614 \cdot r \cdot W^{0.446}) \qquad (27)$$

here

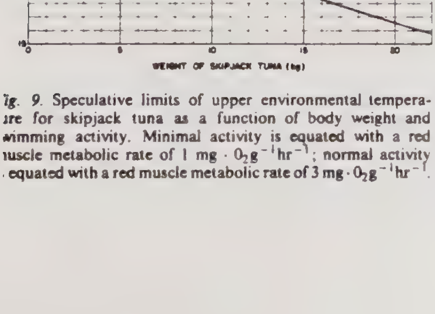
ıax T_a = maximum environmental temperature, °C;

r = metabolic rate of red muscle, mg O_2 g^{-1} hr^{-1}; and

W = fish weight, kg.

he above relation implies that *r* in free-swimming cipjack tuna is independent of *W*, a proposition ıpported by unpublished data collected by R. M. iooding (National Marine Fisheries Service, OAA, Honolulu, HI 96812). Mcreover, we sugest that the equation in present form is equally pplicable to skipjack tuna of all sizes, up to the ıaximum attained — 22 kg, according to Collette : Gibbs (1963).

From the analysis presented in the last section, ıinimum *r* for skipjack tuna red muscle would eem to be about 1.0 mg O_2 g^{-1} hr^{-1}. Solving equaon 27 with r = 1 gives max T_a = 33.4° C at W = kg, max T_a = 30.5° C at W = 10 kg, and max T_a = 28.6° C at W = 22 kg (Fig. 9). In the sense that ven minimal activity could not be sustained at emperatures above max T_a for r = 1, these temeratures are equivalent to typical fishes' incipient pper lethal temperatures (Fry, Hart & Walker 946). (Of course, if some other tissue, such as eural tissue, ceases to function above a temperaıre less than 35° C, then that temperature rather than max T_a becomes limiting for fish smaller than some particular size.)



ig. 9. Speculative limits of upper environmental temperaıre for skipjack tuna as a function of body weight and wimming activity. Minimal activity is equated with a red ıuscle metabolic rate of 1 mg · $O_2 g^{-1} hr^{-1}$; normal activity equated with a red muscle metabolic rate of 3 mg · $O_2 g^{-1} hr^{-1}$.

While r = 1 mg O_2 g^{-1} hr^{-1} may be the physiological minimum for red muscle metabolism in skipjack tuna, the ecological minimum must be higher if the fish is to feed successfully, escape predators, and migrate. In the absence of data, we offer r = r mg O_2 g^{-1} hr^{-1} as the average metabolic rate in the red muscle of normally active skipjack tuna. Limiting upper environmental temperatures then become 30.2° C at W = 1 kg, 21.5° C at W = 10 kg, and 15.8° C at W = 22 kg (Fig. 9).

These calculations imply that large skipjack tuna must occupy cooler waters if they are to be as active as smaller fish. This could be achieved by large fish living at higher latitudes or at greater depths than smaller fish. Low rates of heat exchange in large skipjack tuna would permit forays of several minutes' duration into surface waters warmer than max T_a if the fish were initially at thermal equilibrium with deeper, cooler water.

Simulated tissue temperatures in a school of skipjack tuna at sea

Simulation of body temperatures in time series is a useful adjunct in grasping how effectively large thermal inertia can damp fluctuations of environmental temperature. Such an illustration has been provided for a very large scombrid, the bluefin tuna (Neill & Stevens 1974), but not for smaller fish.

For the skipjack tuna simulation, we chose an environmental temperature series derived from actual observations by Yuen (1967) (see footnote [2]) on the movements of a skipjack tuna school in waters off Oahu, Hawaii. Vertical position of this school of 1.8 kg fish was estimated at 30 sec. intervals from CTFM sonar data (contact distance and tilt angle); target identification as to species and estimated fish size was made visually when the school was near the surface.

From the position estimates and from a concommitant bathythermograph record, we estimated T_a experienced by these fish at 1 min. intervals for the entire 54 min. period during which the school was observed (Fig. 10). Then, assuming appropriate and constant values of *k* and T_x for 1.8 kg skipjack tuna, we simulated thermal responses of red muscle, white muscle, brain, and venous blood by exponentially filter-

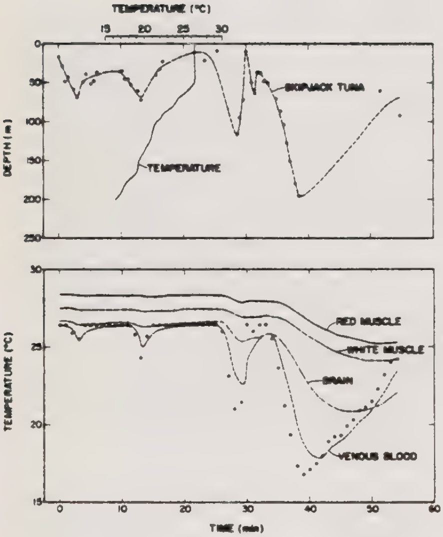


Fig. 10. Vertical movements and simulated tissue temperatures in a school of 1.8 kg skipjack tuna tracked by sonar off the Waianae coast of Oahu, Hawaii. The upper panel gives individual and smoothed sonar 'fixes' on the school's depth position and the concomitant vertical distribution of sea temperature. The lower panel gives estimated environmental temperature at one minute intervals and the time-course of simulated red muscle, white muscle, brain, and venous blood temperatures. The fish were assumed to be in thermal equilibrium with the water at the onset of observation. Parameters of heat exchange used in the simulations were as follows:

Tissue	T_x(° C)	k(° C min^{-1} ° C^{-1})
Red muscle	2.0	0.034
White muscle	1.1	0.038
Brain	0.3	0.114
Venous blood	0.0	0.500

ing the $T_e (= T_a + T_x)$ series:

$$T_{b_i} = T_{e_i} - (T_{e_i} - T_{b_{i-1}})e^{-kl} \qquad (28)$$

where l = 1 min.

The effect of differences in thermal inertia (varied *k*) among tissues was clearly illustrated by the varying magnitude and phase lag of response to T_a decreases that occurred when the fish sounded into the thermocline (Fig. 10). During the deepest dive, T_a decreased to 16.8° C at 39 min.; this 9.6° C decrease in T_a caused hypothetical maximum decreases of 2.5°, 2.9°, 5.0°, and 7.0° C in temperature of red muscle, white muscle, brain, and venous blood, respectively. Whereas minimum venous blood temperature occurred 3 min. after minimum T_a, the equivalent lag was about 11 min. for red muscle, by which time T_a had increased to 23° C.

Thus skipjack tuna even as small as 1.8 kg achieve substantial independence from rapid fluctuations of environmental temperature. In the case of small fish sounding into the cool waters of the thermocline, the musculature would remain relatively warm and, therefore, presumably more efficient for swimming than it would otherwise be. Larger skipjack tuna are potentially able to regulate body temperature within narrow limits by low-frequency vertical movements within the thermocline or between the upper mixed layer and the thermocline.

Inertial storage of thermal information: a hypothesized mechanism for perception of weak temperature gradients

It now appears that tunas as a group are no more responsive to abrupt changes of temperature than are other fishes (Dizon et al. 1974; Steffel et al., MS.[3]). Smallest discrimination thresholds for temperature change in a scombrid were those obtained by Steffel et al. (MS.[3]) for free-swimming kawakawa; two instrumentally conditioned fish responded to abrupt temperature increases as small as 0.10° and 0.125° C, respectively. Thresholds no smaller than 0.1° C preclude directed orientation (klinotaxis or tropotaxis; see Fraenkel & Gunn 1961) to even the more steep horizontal gradients of the open sea (0.0001 to 0.001° C m^{-1}).

Yet, the evidence for a cause-effect relationship between temperature and tuna distribution is convincing (Howard 1963; Laevastu & Rosa 1963; Broadhead & Barrett 1964; Blackburn 1965). How do tunas, with only ordinary sensitivity to abrupt changes of temperature, behaviorally thermoregulate in an environment whose temperature-

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[3] Steffel, S., A. E. Dizon, J. J. Magnuson & W. H. Neill. Temperature discrimination by captive free-swimming tuna, *Euthynnus affinis*. Manuscript in preparation. Laboratory of Limnology, University of Wisconsin, Madison, WI 53706.

ange signals are much weaker than those avail-
le to freshwater and inshore marine fishes? The
swer to this question may involve tuna's rela-
ely large thermal inertia, in the role of a simple
mperature 'memory' mechanism.

Inertial memory of the recent thermal environ-
ent is contingent on perception of the instan-a-
ous difference between body-core and ambient
mperatures. This difference will increase for
h swimming into cooler water and decrease for
h swimming into warmer water. The magni-
de of the difference depends on the coefficient
core-temperature change, the time-rate of
nbient temperature change (which in turn
pends on slope of the gradient and speed of
imming: $dT/ds \cdot ds/dt = dT/dt$), and the tem-
oral persistence of the particular time-rate of
ange. Largest differences will develop for
rge fish (which swim fast and have small *k*'s)
imming for long periods of time perpendicular
isotherms in steep temperature gradients. In
hes like tunas, which maintain excess core
mperatures, the difference consists of two com-
onents, one the equilibrium excess and the
ther a non-equilibrium difference attributable
thermal lag. In order that the temperature
ifference $T_b - T_a$ provide environmental in-
ormation, the fish must be able to separate the
omponents of difference; i.e., the fish must
now' the value of T_e to properly partition the
ifference, $T_b - T_a$:

$$_b - T_a = (T_b - T_e) + (T_e - T_a), \qquad (29)$$

here
$_b - T_e$ is the non-equilibrium difference, a func-
on of *k* and changing ambient temperature; and,
$_e - T_a$ is the equilibrium excess temperature, T_x,
function of metabolic rate and *k*.

equisite 'knowledge' of T_e might be achieved
uite simply, through a neural transformation of
ome metabolic correlate, such as tail-beat rate
A):

$$_e = T_a + f(A, k) = T_a + T_x. \qquad (30)$$

That fishes can make adjustments in behavior that
ompensate for variations in metabolism is con-
irmed by Rozin (1964), who showed that temporal
iscrimination in goldfish, *Carassius auratus* (Lin-
aeus), is independent of metabolic changes ac-
ompanying shifts in environmental temperature.

For linear gradients of temperature in which a fish swims at constant speed with constant metabolic rate, it follows from equation 1 that

$$T_b - T_e = -s \cdot G/k \cdot [1 - e^{-kt}] \qquad (31)$$

where

$T_b = T_e$ at $t = 0$;
s is swimming speed;
G is slope of the temperature gradient;
k is the coefficient of core-temperature change; and, t is time.

By way of example, we have considered a skipjack tuna, 47 cm long and weighing 2 kg, swimming at 1.77 bl $sec.^{-1}$ (50 m $min.^{-1}$) into a linear temperature gradient of $-0.001°\ C\ m^{-1}$ (Fig. 11). Red muscle of the fish has *k* and T_x of $0.033°\ C\ min.^{-1}\ °C^{-1}$ and 2° C, respectively, both of which are invariate. At $t = 0$, the fish enters the gradient in thermal equilibrium. After 10 min. (0.5 km into the gradient), $T_b - T_e$ is $+0.43°$ C; after 30 min. (1.5 km), $T_b - T_e$ is $+0.95°$ C; and, after 100 min. (5 km), $T_b - T_e$ is $+1.46°$ C, only 0.06° C short of the asymptotic value of $+1.52°$ C.

We suggest that fishes may perceive the difference, $T_b - T_e$, and use it as the basis for klinokinetic (Fraenkel & Gunn 1961) orientation responses that comprise behavioral thermoregulation. For typical fishes, $T_e \simeq T_a$; thus, the fish need

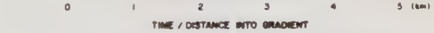

Fig. 11. Time-series simulation of red muscle temperature in a 2 kg, 47 cm long skipjack tuna swimming at 50 m min^{-1} (1.77 body lengths sec^{-1}) into a $-0.001°\ C\ m^{-1}$ temperature gradient. Thermal inertia results in the development of a difference between actual and equilibrium red muscle temperatures; such a difference may constitute the basis for perception of weak temperature gradients in tunas and other fishes. (Heat exchange parameters used in the simulation were $T_x = 2.0°$ C and $k = 0.033°\ C\ min^{-1}\ °\ C^{-1}$.)

only make a simple comparison between temperatures sensed at the water-fish interface and somewhere in the body core. To obtain the same information, scombrids must have a mechanism such as that suggested above whereby $T_b - T_a$ is 'corrected' for the contribution of varying heat production; that is, their 'comparator' must be continuously offset by the variable amount, T_x. But, the heat exchanger of scombrids, in part responsible for this complication, also confers on these fishes a distinct advantage: Gradients so gentle as to be otherwise imperceptible are in effect amplified by a factor of about 2. Thus, the skipjack tuna considered in the above example could theoretically detect a temperature gradient as weak as ±0.000066° C m^{-1} (±0.066° C km^{-1}) if it were sensitive to an instantaneous difference, $T_b - T_e$, as small as ±0.1° C. A fish without the heat exchanger but otherwise the same could theoretically detect a temperature gradient only as weak as ±0.00011° C m^{-1} (±0.11° C km^{-1}).

Another of the heat exchanger's possible benefits in thermo-perception is that thermal information derived from the difference $T_b - T_a$ is spatially condensed over the short distance separating the ends of the exchanger vessels — only about 10 mm in a 2 kg skipjack tuna (Stevens, Lam & Kendall 1974). Such sharp gradients cannot occur in fishes without specialized heat exchangers.

We can offer little evidence that body temperature differentials are in fact used by fishes in perception of gradients. Perhaps the most direct support for the hypothesis comes from observations by Peterson & Anderson (1969) on spontaneous activity of Atlantic salmon, *Salmo salar* Linnaeus, exposed to temperature changes. Activity peaks lagged initial changes of ambient temperature by several minutes. E. D. Stevens (University of Hawaii, Honolulu) and the senior author have simulated body temperatures of these fish by the methods described above; peaks of activity generally were simultaneous with estimated maximum values of $|T_b - T_e|$. Faster changes of water temperature over the same span of temperature produced larger values of $|T_b - T_e|$ and greater peak levels of activity.

There appear to be no published data contrary to the hypothesis. Certainly, the results of experiments on discrimination of temperature changes by fishes (e.g., Bull 1936; Bardach & Bjorklund 1957; Dizon et al. 1974; Steffel et al. MS.[3]) do not deny the possibility that discriminating subjects were perceiving abrupt increases in $|T_b - T_e|$ rather than temporal or spatial variation in T_a. Arctic sculpins of the genus *Myoxocephalus* exhibit overt escape behavior upon transfer to warm water only when the body core reaches a specific temperature (Hammel, Strømme & Myhre 1969), in apparent disregard for the difference $T_b - T_e$; however, there is nothing about these results to suggest that perception of the temperature step-change, minimally 7° C, did not occur the moment of transfer to warmer water. In similar experiments with two antarctic fishes, *Notothenia coriiceps* and *Chaenocephalus aceratus*, escape behavior appeared after a time lag inversely proportional to magnitude of the temperature change (Crawshaw & Hammel 1971).

Conclusion: ecological benefits and costs of large thermal inertia for skipjack tuna

Heat exchange between the core of skipjack tuna and the environment is retarded by a highly efficient countercurrent heat exchanger in the blood-vascular system. The resultant augmentation of thermal inertia, together with a high metabolic rate, makes skipjack tuna perhaps the warmest of 'warm-bodied' fishes on a per weight basis.

Our experiments provided no evidence that skipjack tuna regulate the efficiency of heat exchange, thereby achieving the capability for physiological thermoregulation. Rather than regulating body temperature as do mammals and birds or metabolically conforming to environmental temperature as do typical fishes, skipjack tuna apparently have adopted a third strategy of thermal adaptation — metabolic near-independence from temperature (Gordon 1968).

Why, then, have skipjack tuna made the evolutionary investment in a countercurrent heat exchanger, if not for use in rapid regulation of core temperature? One possibility is that the skipjack's heat exchanger functions only in long-term (weeks or months) physiological thermoregulation about which we have as yet no information. A second possibility is that the enzymatic systems compatible with high metabolic rates and evolutionarily available to the skipjack tuna are intrinsically more efficient at temperatures somewhat higher than those of the tropical seas; thus, because elevated body temperatures are adaptive, large thermal inertia is adaptive. Another is that the heat ex-

nger protects the muscle mass from rapid
nges of temperature and from short-term ex-
ure to extreme temperatures, both of which
ht damage the muscle or lessen its efficiency of
ration; in this sense, large thermal inertia
ances behavioral thermoregulation, both by
reasing the effectiveness of correct responses
by lessening the consequences of mistakes.
ally, increased thermal inertia may be im-
tant in perception of the weak horizontal gra-
nts of temperature that characterize the high-
s habitat of skipjack tuna.

Whatever the benefits of large thermal inertia
skipjack tuna, they must be sufficient to offset
at we suggest is a major ecological cost —risk of
erheating the muscle mass, especially during
riods of high activity in warm water. Excess core
uilibrium temperatures presumably increase
th fish size; so, skipjack tuna must seek out
oler and cooler water as they grow larger. In
eas where surface waters are too warm for con-
uous occupancy by skipjack tuna of a given
e, the fish probably adopt a cyclical pattern of
pth distribution, alternately rising to the surface
feed or navigate and sounding into the thermo-
ine to cool.

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HISTOLOGICAL CRITERIA FOR DIAGNOSING THE STARVING CONDITION IN EARLY POST YOLK SAC LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX* Girard

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Abstract: The identification of fish larvae that are in starving condition in plankton samples would be a valuable aid in estimating early mortality rates of populations in the sea. Histological criteria are given for determining the degree of starvation-induced emaciation, with an indication of its relevance to mortality, for larvae of the northern anchovy, *Engraulis mordax* Girard. Larvae were reared with and without food to age 9 days, *i.e.*, beyond the point of yolk absorption.

Eleven histological characteristics were each graded on scales of poor, intermediate or good, depending variously on texture, shape and fullness of nuclei, cytoplasm, extracellular substance, and cellular products and storage material. Grades varied with food deprivation, so that increasing emaciation may be estimated from histological variables. Distribution of the grades also paralleled trends in survival and length, indicating that degree of emaciation reflects the probability of survival.

The histological variables that best classified larvae as severely emaciated, moderately emaciated, or robust in a stepwise discriminant analysis were pancreas condition, trunk muscle fiber separation, intermuscular tissue, and liver cytoplasm. The discriminant analysis suggests that an average of grades for three or four characteristics is sufficient for determining the state of emaciation of a larva.

INTRODUCTION

In attempting to understand the causes of fluctuations in year-class size of marine teleosts, Hjort (1914, 1926) proposed the concept of a critical period, according to which the strength of a year class is largely determined by survival of the larvae immediately after yolk is exhausted and so probably depends on the availability of planktonic food at that time. May (1974) concluded from a review of both laboratory and field studies since the time of Hjort that while the relation between year-class strength and early mortality remains unclear, starvation beyond the end of the yolk sac stage could be an important cause, both directly and indirectly, of larval mortality. Evidence of starving larvae in the sea is, however, slight and this is due in part at least to difficulties in diagnosing the starving condition. Condition factor (wt/l^3) (Blaxter, 1971) and chemical indices (Ehrlich, 1974) both show changes with starvation in herring and plaice but are complicated by problems of measurement and changes with growth. Morphometric methods showed some possibilities for the anchovy (Nakaii *et al.*, 1969) and the plaice (Shelbourne, 1957), and recently have been used to characterize the progressive collapse of the head and pectoral region of starving herring and plaice larvae (Ehrlich, Blaxter & Pemberton, 1976). Some histological changes were also described in the latter study, and a histological approach was used by Umeda & Ochiai (1975) to classify laboratory-reared larvae of the yellowtail, *Seriola quinqueradiata*, on the basis of condition of the cells of the digestive tract, liver and pancreas into feeding, semi-starved, and starved types.

In the present study, criteria for judging starvation in first-feeding larvae of the northern anchovy, *Engraulis mordax* Girard, are based on histological changes rather than on morphometrics. There can be little doubt that morphological characteristics change with starvation and that they are relatively simple to measure, but there is uncertainty in regard to the validity of laboratory derived criteria for populations in nature. Body proportions and condition factor have been shown to differ for laboratory reared and wild herring down to lengths of 16 mm (Blaxter, 1971; Balbontin, De Silva & Ehrlich, 1973). It is, however, difficult to establish criteria except by laboratory rearing, where changes can be related to food deprivation and survival. The histological approach appeared to hold good possibilities for developing criteria based on deterioration of cell and tissue structure and integrity that would be largely free of dimensional considerations, and fundamentally the same for laboratory-reared and ocean-caught animals.

In addition to the kinds of degeneration described by Umeda & Ochiai (1975) for the digestive tract and its associated glands, the decrease in protein and relative increase in water content that might be expected to accompany starvation were considered likely sources of histological indicators. Love (1974) states that cell size in several animals decreases and extracellular space increases as the relative water content rises during starvation. This has been demonstrated histologically for the trunk musculature of mature cod, *Gadus morhua* (Love, Robertson & Strachan, 1968), and the rough dab, *Hippoglossoides platessoides* (Templeman & Andrews, 1956). Love (1974) found that in such cases muscle protein is not mobilized until relatively late in starvation, after lipid reserves have been depleted, but as Ehrlich (1974) has shown for both herring and plaice, early larvae have negligible lipid reserves, and protein mobilization starts immediately on starvation.

MATERIALS AND METHODS

Eggs were collected early in the morning following night-time spawning in the aquarium of the Southwest Fisheries Center (SWFC) of a captive school of the northern anchovy, *Engraulis mordax*. Spawning was induced by gonadotropin injections (Leong, 1971). The eggs were incubated for 24 h at 16 °C, when 100 eggs showing normal development were transferred by pipette to each of 16 glass beakers containing 3200 ml of sea water. The beakers were held in a water bath at 17 °C (± 0.5 °C) under a 12-h light, 12-h dark cycle. A dim light remained on during the dark phase.

Hatching was largely completed 72 h after eggs had been collected, *i.e.*, 48 h after they had been put in the glass beakers. The time at which the larvae were ≈ 24 h old, was designated as the start of day 1 in the life of the larvae.

One half of the larvae were fed, the other half were starved. On day 1 all fed larvae received *Gymnodinium splendens* at a density of ≈ 150/ml as initial diet food (Lasker *et al.*, 1970). At the start of day 3 the rotifer *Brachionus plicatilis* was added as a second food (Theilacker & McMaster, 1971) at a density of ≈ 100/ml; the densities of these organisms were estimated every other day and supplements were added to maintain the initial levels.

Dead eggs and larvae were removed by pipette and counted on day 1. On all subsequent days, dead larvae that were readily detected were removed, but not counted.

Samples of larvae on each successive day from age 2 days were obtained by sacrificing the entire remaining population from one container in the fed series and one in the starved series. After the readily visible dead larvae were removed, the living ones were captured one or a few at a time by pipette or small beaker and immediately dropped into Bouin's fluid or in some cases 10 % buffered neutral formalin. Each larva preserved was alive at the time of capture.

Two to 4 days after fixation, the fixing fluid was replaced by two changes of 70 % ethyl alcohol at 24 h intervals. Larvae were then measured and stored individually in small vials of 70 % ethyl alcohol. Less than 2 weeks after fixation all larvae were dehydrated and embedded in 56° to 57 °C Paraplast *plus*. Dehydration was carried out automatically in a Fisher Tissuematon with an ethyl alcohol–*n*-butyl alcohol series, the final solution being pure *n*-butyl alcohol (three changes).

Larvae were serially sectioned at 6 μm approximately in the sagittal plane, mounted, and stained in Harris's hematoxylin–Eosin. Coverslips were mounted with a synthetic resin medium. The plane of sectioning was only approximate because no attempt was made to straighten larvae before or during the embedding step. Although most larvae were straight or nearly so, some had strong lateral bends; for these the sectioning plane tended to be frontal. Larvae were not forcibly straightened for measurement, although they were placed on a wet slide where most assumed a reasonably straight posture. For those with noticeable bends, standard length was measured in successive increments. About 10 % of all larvae were too irregular to be measured.

The microscopic examination of larvae was carried out in two stages. First, the largest and the smallest individual from the fed and starved groups terminated on each of the days, 3 through 6, were separated from the collection and labelled with random numbers to mask their identity. Examination of this group of 16 specimens, presumed to represent the extremes of variability *vis à vis* the availability and non-availability of food, indicated the features that should be examined in all and also suggested a format for the examination. Following this preliminary study, the remaining 204 fixed specimens were randomly labelled for examination.

RESULTS

SURVIVAL

Lasker *et al.* (1970) showed that populations of anchovy larvae reared at 22 °C declined only moderately over 12 days in the presence of food, but suffered almost total mortality after 6 days if starved. They further established a "point of no return," *i.e.*, the latest time that food must be made available if the larvae were to have a good chance of surviving, at age 3 days, which was 2 days before increased mortality appeared and 3 days before it was virtually total in the absence of food. Ages 4 and 5 days were, therefore, considered to constitute a period of irreversible starvation for larvae that had not yet received food. In the present work, survival is given by the percentage of the initial population recovered on the day it was terminated and harvested:

Day	2	3	4	5	6	7	8	9
Fed	57	51	72	55	75	71	27	42
Starved	56	56	48	38	40	11	0	0

The initial populations were determined from the numbers of eggs originally introduced (100) minus the numbers that were found dead and unhatched, along with some dead larvae, on day 1 ($\leqslant$ 22 for most containers). In the starved series, mortality was very high on day 7 and total on day 8. This was preceded by slightly increased mortality on days 5 and 6. These events occur a day later than shown by Lasker *et al.* (1970), undoubtedly because this experiment was carried out at a temperature of 17 °C *i.e.*, about 5 °C lower, and so 7 days is considered here to be the age at which there is high mortality from starvation, while 5 to 6 days is the period during which many larvae reach a state of irreversible starvation. In the fed series, moderately good proportions of larvae survived in all containers, but it does appear that there was some increase in mortality at or just after day 7, the time when populations without food rapidly died. This pattern resembles those arising when food densities are inadequate (O'Connell & Raymond, 1970), or when food introduction is delayed (Lasker *et al.*, 1970).

LENGTH

The mean and range of standard length is shown in Fig. 1 for each of the age-food treatment groups. These data are based on about half of the larvae removed from containers at termination and fixed in Bouin's fluid. The others were fixed in formalin. Comparison of standard length measurements, taken after fixation, showed that the Bouin-fixed material adequately represented the length range for each of the container populations. One point of interest is that the Bouin-fixed material was consistently about 6 % less than the formalin-fixed material.

The mean length of fed larvae increased more or less steadily, with the greatest increase between 5 and 7 days. The means and ranges agree closely with those given by Kramer & Zweifel (1970), except at day 9 where it was 20 % lower, indicating that the growth of fed larvae was suboptimal during the last day or two. For the starved larvae, mean length tended to decrease, especially between age 5 and 6 days, to a point much lower than that for fed larvae at day 6. The decreasing mean length with age for the starved groups may be assumed to represent shrinkage, which has been shown to occur in starved herring larvae after yolk absorption (Blaxter & Hempel, 1963).

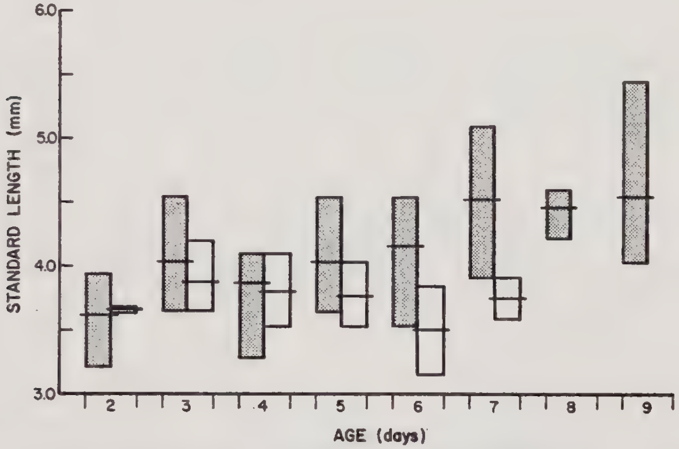


Fig. 1. The mean and range of standard length for larvae preserved from each of the age-food groups: dark bars, fed; light bars, starved.

Although increase in length is adversely affected by starvation, it must be noted that a large proportion of larvae in the 5 to 7 day old starvation groups would not be distinguishable from many of the larvae in fed groups of various ages on the basis of length alone. The ranges are broadly overlapping among all groups.

In addition to standard length other measurements were made on the formalin-fixed larvae to determine whether body proportions changed in relation to food deprivation. Dorsal finfold depth, body depth (including the digestive tract), and ventral finfold depth were measured at the level of the pyloric valve. Midgut length was measured as the distance from the pyloric valve to the ileo-caecal constriction, and hindgut length as the distance from the latter to the tip of the anus. The averages of these measurements were constant proportions of standard length over all age-food treatment groups. None of these proportions could be used to diagnose the starving condition over the first 9 days of life. The morphometric features, pectoral angle and the eye height: head height ratio, shown to change with starvation for herring and plaice larvae by Ehrlich, Blaxter & Pemberton (1976), were not measured on the above anchovy larvae. In view of their small size, it is uncertain whether these anchovies would have shown changes with starvation in such measurements. The largest fed animals were no more than 5.5 mm S.L. at age 9 days, and the largest starved ones no more than 4.5 mm S.L. The morphological changes were not distinguishable for herring < 2 weeks old and 10 mm S.L. These measurements might give useful indications of starvation for more advanced anchovy larvae.

HISTOLOGICAL VARIATION

Ultimately, 11 histological variables were used to analyse the differences relative to starvation. These were characteristics of the notochord, cartilage, trunk musculature, digestive tract, liver, and pancreas, all of which show growth and differentiation but no striking changes in morphological organization between the ages of 2 and 9 days. General descriptions are given below, followed by an outline of the criteria used in grading the observed variability.

Notochord. The notochord, composed of vesicular connective tissue in which fluid-filled vacuoles predominate, is by far the largest tubular structure of the body. The spinal cord lies along its dorsal midline and the dorsal aorta along its ventral midline. It is encircled by a layer of transverse bands which eventually form the outer sheath of dense fibrous connective tissue. Generally the notochord is turgid and fully distended, but it can show degrees of collapse.

Cartilage. The jaws and branchial elements, along with certain pectoral girdle and cranial elements, have the characteristics of procartilage, the elements being composed of chondrocytes in close proximity, separated by no more than thin shells of capsular or territorial matrix. The appearance of inter-territorial matrix and the consequent separation of chondrocytes starts at age 8 or 9 days. During the procartilage stage the basophilic chondrocytes ordinarily have round, light granular or mottled nuclei and lightly stained cytoplasm which largely or entirely fills the capsular spaces; however, nuclei can be small and dense and cytoplasm partially or completely lacking.

Trunk musculature. The trunk musculature is closely applied to the lateral surfaces of the notochord between the spinal cord and the dorsal aorta. It is segmented, the myomeres having a weak chevron form and overlapping slightly; the layer is, nevertheless, relatively thin during this early period. The major components of the trunk musculature are a layer of internal oblique fibers (antero-ventral to postero-dorsal) and a layer of external oblique fibers (opposite alignment). The fibers, which contain a number of axial nuclei surrounded by myofibrils that run the full length of the fiber, are broadly attached to the myosepta, but they are precisely aligned in successive myomeres to form fiber trajectories that apparently extend over two to three myomeres. Striations are evident in the fibers. Within each myomere the internal and external oblique layers are separated by a moderately thick layer of basophilic substance with a light granular texture and scattered nuclei. The granular substance appears to be cellular cytoplasm, and this intercellular layer is probably composed mainly of myoblasts. The muscle fibers themselves may vary both in width and lateral separation and the intermuscular tissue may vary from thick and relatively dense to virtually complete absence.

By the end of the first week an outer or superficial layer of slender, horizontal muscle fibers is visible over the entire surface of each myomere. The lateralis branch of the vagus nerve, which subtends the lateral line of neuromasts, lies between the superficial muscle layer and the epidermal integument. The superficial muscle layer and neuromasts were not involved in evaluating the condition of larvae.

The digestive tract. The digestive tract is composed of a long foregut, a straight midgut of lesser length but greater diameter, and a short hindgut. The foregut is made up of cuboidal mucosa cells and a coat of transverse muscle fibers. The mucosa shows weak longitudinal ridges over its entire length. It is stratified and folded at the pharyngeal port, where the only goblet cells in the digestive tract are found. Although there was some variation in size and clarity of mucosa cells and in the mass of the pharyngeal port tissue, the range of variation was small and no attempt was made to evaluate the foregut. It should be noted that the anchovy larva does not have a stomach, in either the morphological or glandular sense, until much later in its development.

Transition to the midgut at the pyloric port involves an increase in cell height and in longitudinal folds that reduce the lumen to valvular proportions. The midgut mucosa is composed of one type of columnar cell with microvilli on the mesial border facing the lumen. Cytoplasm tends to be homogeneous and lightly granular, but sometimes has a coarse, dark appearance. Cells are closely joined laterally and nuclei are in the basal half so that, in tangential section, the apical halves generally form a well defined unnucleated mosaic. At age 2 days the lumen surface of the midgut mucosa is essentially flat, although there may be some degree of longitudinal folding. The mucosa cells are somewhat shortened when the lumen is well expanded. The strong transverse folds characteristic of the species begin to take form at days 8 and 9.

The chief indicators used in evaluating the midgut were the texture and color of the cytoplasm, the prominence of the tangential mosaic pattern, or conversely the tendency for mucosa cells to be separated rather than well joined; the band of microvilli did not seem to vary. The midgut showed vacuolization and hypertrophic cells in a small number of specimens. These conditions were recorded and will be discussed later.

Transition to the hindgut is marked by a low ileocaecal ridge, visible from the exterior in many larvae as a shallow furrow. The cells of the hindgut mucosa did not differ in appearance from those of the midgut except for the presence of supranuclear eosinophilic inclusion bodies in many feeding larvae. Evaluation of the hindgut was based on the absence or presence and extent of such inclusions which could be considerably larger than the cell nuclei and very abundant.

Iwai (1968, 1969) and Iwai & Tanaka (1968) described inclusion bodies in the hindgut of larvae of some freshwater teleosts and suggested that these were indicative of intracellular digestion of food particles engulfed by pinocytosis in the hindgut. Though it may occur, pinocytosis was not identified in the hindgut of the anchovy larva. The biochemical composition of the inclusions is uncertain. A few dozen formalin-fixed specimens were post-fixed in osmium tetroxide, which stains several kinds of lipid droplets black (Chang, Lalich & Alden, 1974). Hindgut inclusions in these larvae were strikingly black, but no structures in the midgut mucosa gave this reaction. This tentative result contrasts with the finding of Iwai that hindgut inclusions in the larvae studied by him were probably proteinaceous (electron lucent) and that lipid droplets occurred in the midgut mucosa.

The liver. The two large glands of the digestive tract, liver and pancreas, are elongate, compact organs beneath and partially surrounding the posterior half or more of the foregut. Both give ducts into the pyloric region of the midgut along with the cystic duct extending from the gall bladder, which is a cylindrical, membraneous structure lying between, and somewhat rostral, of the anterior ends of the liver and pancreas. The gall bladder, always visible and at least moderately well distended, was measured but not otherwise graded.

The liver is composed of close-packed tubules of pyramidal hepatocytes. The tubule lumina, sometimes clearly visible, are short projections from the hepatic vein which traverses the organ longitudinally. The dilation of the hepatic vein and tubules was often difficult to judge, so this feature was not graded. Both the nuclei and the cytoplasm of the hepatocytes showed considerable variability. Nuclei most often contained a distinct nucleolus with relatively few surrounding dark granules, but in some specimens the dark granules were widespread, sometimes submerging the nucleolus or even occupying the entire nucleus. It is possible that the relative amount of dark material indicates the extent to which chromatin is 'condensed' and not actively synthesizing RNA and ultimately protein (Stein, Stein & Kleinsmith, 1975). At worst, nuclei became pycnotic, *i.e.*, black and irregular. Cytoplasm was hyaline in some specimens, uniformly or irregularly granular in others, and dispersed in yet others. The dispersed state accompanied clear intracellular spaces of considerable size. Intracellular spaces sometimes occurred when the cytoplasm was more homogeneous, but then the spaces were small and generally infrequent. Presumably the intracellular spaces are sites of glycogen or lipid storage in the liver.

The pancreas. The exocrine pancreas, lying along the right side of the foregut and occasionally extending rostral of the gall bladder, is composed of pyramidal acinar cells surrounding the terminal branches of a pancreatic duct system. In the early anchovy larva the branches are not discernible and are probably in an early stage of budding from the axial main duct, part of which is visible as a relatively large, more or less spherical sinus in the posterior half of the organ. The sinus was usually filled with homogeneous zymogen, probably available for immediate transport to the midgut. There was wide variation in the state of fullness of the sinus and this feature as well as the pancreas proper was graded.

In the pancreas proper the basal part of the pancreatic acinar cells contain, along with the cell nucleus, strongly basophilic ergastoplasm or chromaffin. The apices of the cells contain membrane bound droplets of zymogen (acidophilic). Zymogen is synthesized in the ergastoplasm, concentrated in the Golgi apparatus above the ergastoplasm, and accumulated in the apical region, from which it is secreted into the acinar ducts by fusion of the droplet membranes with the cell membrane (Bloom & Fawcett, 1968). For a number of vertebrates it has been shown that the production of zymogen tends to vary with the intake of food (Bloom & Fawcett, *loc. cit.;* Patt & Patt, 1969). In the resting and/or fasting state accumulated zymogen is prominent and chromaffin minimal. Following a large meal, zymogen is reduced and the chromaffin becomes more prominent as the rate of synthesis increases. Although cyclic patterns were not found, the anchovy larva showed considerable variation in the relative prominence of zymogen and chromaffin. The pancreas was graded with respect to this variability as well as on indications of cell diminution and separation.

The endocrine pancreas is a single large Islet of Langerhans located immediately behind the sinus of the pancreatic duct. Although the condition of the Islet tended to vary with the condition of the organ, it was not graded as a separate feature.

Grading of variability

Differences in each of the 11 characteristics studied were graded as 1) poor, 2) intermediate, and 3) good. For a few of the features intermediate grade were used. The grade for a characteristic was based on its appearance in all sections of the larva in which it occurred. Larvae were never identified as to age and food treatment before the grades were assigned; indeed, the majority of larvae were not identified until all examinations were completed. The grading scales were as follows:

Notochord shrinkage:

1. *Severe*; notochord extensively shrunken away from surrounding trunk musculature (Fig. 2).
2. *Medium*; some areas of separation, but most of notochord surface in contact with musculature (Figs 3, 27).
3. *Negligible*; virtually no separation of notochord and muscle (Fig. 4).

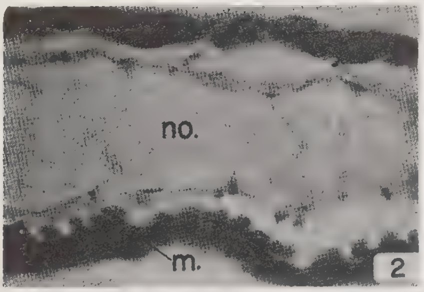
Cartilage:

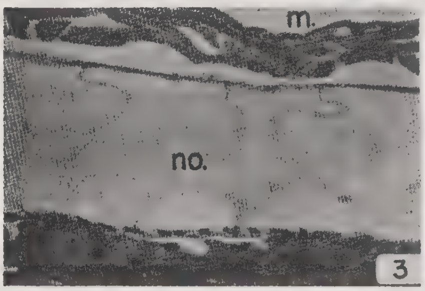
1. *Poor*; nuclei condensed, irregular, cytoplasm largely or entirely absent: this condition was characterized by considerable empty space since the framework of capsular shells did not collapse along with the chondrocytes (Fig. 5).
2. *Intermediate*; nuclei with variable degrees of condensation, presence of cytoplasm variable and often contracted to occupy only a portion of the capsular space (Fig. 6).
3. *Good*; nuclei relatively round and granular, or mottled; capsular spaces largely filled with cytoplasm (Fig. 7).

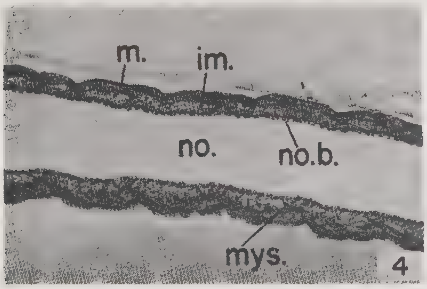
Trunk musculature:

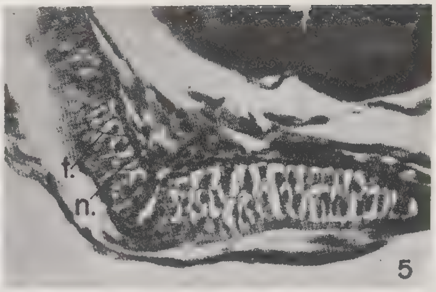
Fiber separation

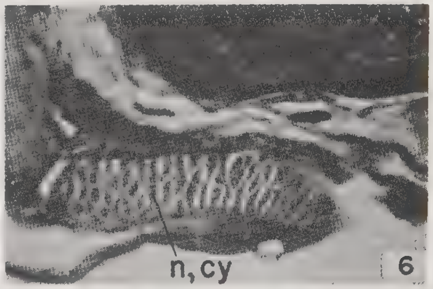
1. *Severe*; parallel fibers separated by wide spaces, sometimes in disarray; fibrils within the fibers indistinct (Figs 8, 9).
2. *Intermediate*; parallel fibers separated by narrow spaces over much of larva; fibrils within fibers distinct (Figs 10, 27).











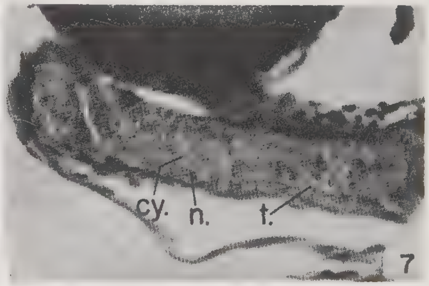


Fig. 2. Severe notochord shrinkage: 6S-1: ×393. The designations are the same in all figures: the first number refers to age, the last to grading, and the letter indicates whether starved or fed, *i.e.* 6S-1 denotes six day larva, starved, condition grade 1.

Fig. 3. Medium notochord shrinkage: 5F-2: muscle fiber shrinkage and intermuscular tissue also medium: ×393.

Fig. 4. Negligible notochord shrinkage: 6F-3: also negligible muscle fiber separation and abundant intermuscular tissue: note prominent transverse bands that become the perichordal sheath: ×155.

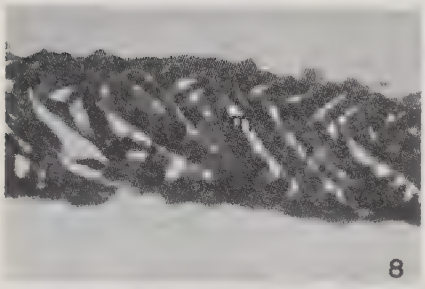
Fig. 5. Cartilage in poor condition: 6S-1: nuclei pycnotic and cytoplasm lacking: ×393.

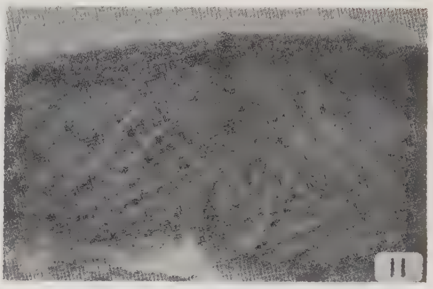
Fig. 6. Cartilage in intermediate condition: 2F-1: nuclei tending to pycnotic, cytoplasm reduced: ×393.

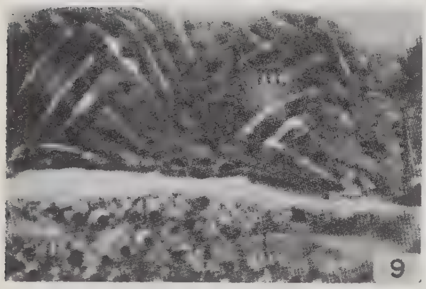
Fig. 7. Cartilage in good condition: 6F-3: ×393.

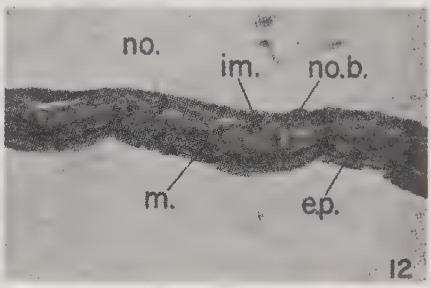
cy., cytoplasm; im., intermuscular tissue; m., muscle; mys., myoseptum; n., nucleus; no., notochord; no. b., bands of notochord sheath; t., territorial matrix of cartilage.

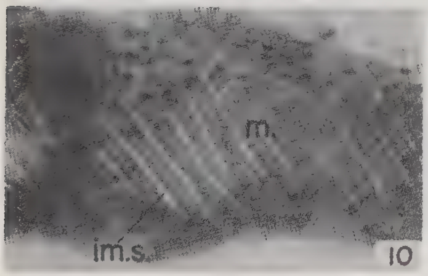
3. *Negligible*; parallel fibers largely in contact laterally; fibrils within fibers distinct; transverse striations usually detectable in any of the three conditions (Fig. 11).











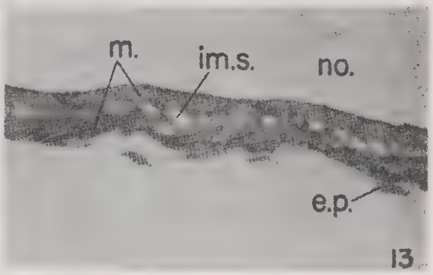


Fig. 8. Severe muscle fiber separation and lack of intermuscular tissue: 6S-1: note loss of integrity of myofibrils within fibers: tan: ×393.

Fig. 9. Severe muscle fiber separation and lack of intermuscular tissue: tan for muscles: 6F-1: ×393.

Fig. 10. Intermediate muscle fiber separation: intermuscular tissue lacking: 5S-1: tan: ×393.

Fig. 11. Negligible muscle fiber separation: 5F-3: note distinct myofibrils in this and previous Fig.: transverse striations present but faint and did not register well: tan: ×393.

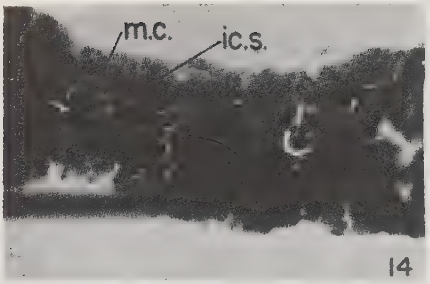
Fig. 12. Thick intermuscular tissue between the two layers of muscle fibers: 6F-3: also both negligible muscle fiber separation and notochord shrinkage: ×393.

Fig. 13. Medium intermuscular tissue, but muscle fiber separation and notochord shrinkage are negligible: 3F-2: ×393.

e.p., epithelial plates; im., intermuscular tissue; im. s., intermuscular space; l., liver; l.l., lateral line neuromast; m., muscle; no., notochord; no. b., bands of notochord sheath; p., pancreas.

Intermuscular tissue

1. *None*; the two layers of muscle separated by some open space; scattered nuclei sometimes visible in spaces (Figs 8, 9).
2. *Medium*; basophilic tissue present between muscle fiber layers but sparse and largely lacking in granular substance (cytoplasm) (Figs 13, 27).



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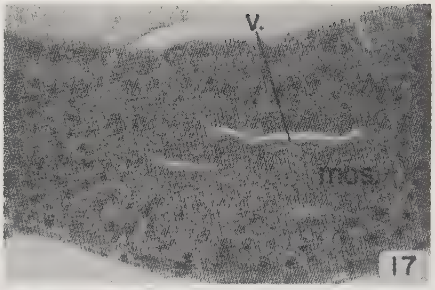

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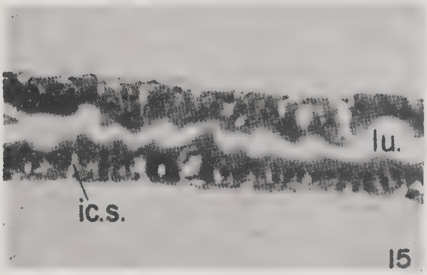

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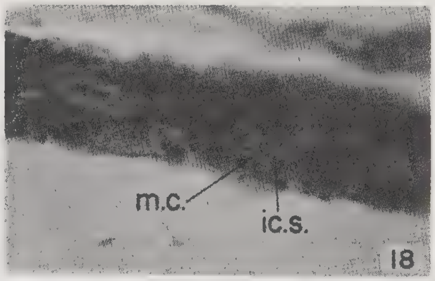

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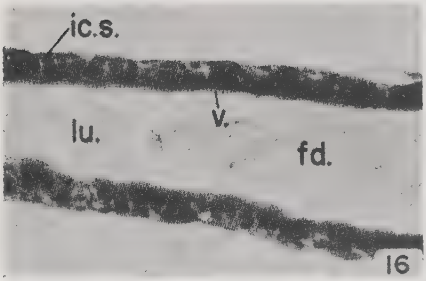

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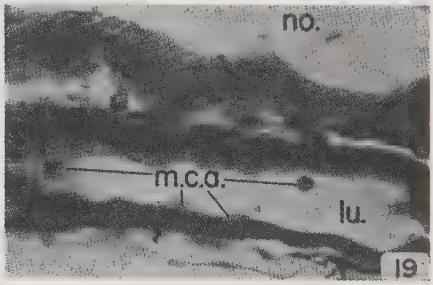

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Fig. 14. Poor midgut integrity: cells are dark and separating: 6F-1: tan: ×393.

Fig. 15. Poor midgut integrity. Spaces are cell separations, not vacuoles: 9F-2: ×393.

Fig. 16. Intermediate midgut integrity: separations are of a lesser degree than above: 3F-2: food in lumen has appreciable chromatophore content: ×393.

Fig. 17. Good midgut integrity: tall, well joined mucosa cells produce a mosaic pattern at the supranuclear level: 5F-3: tan: ×393.

Fig. 18. Intermediate midgut integrity: mucosa cells in early stages of separation: 5S-2: tan: ×393.

Fig. 19. Intermediate midgut integrity: mucosa cells somewhat reduced in size: atrophy shown by sloughing cells: 5S-2: ×393.

fd., food; ic.s., intercellular space; lu., lumen; mos., supranuclear mosaic pattern; m.c., mucosa cell; m.c.a., mucosa cells in atrophy; no., notochord; v., microvilli.

3. *Abundant*; basophilic tissue relatively thick and uniformly present between muscle fiber layers; nuclei common (Fig. 12).

Digestive tract:

Midgut integrity

1. *Poor*; cells tend to be small, dark, and separated (Figs 14, 15).
2. *Intermediate*; tangential mosaic pattern at supranuclear level of mucosa cells

indistinct or absent; separations appearing especially between basal (outer) portions of cells; cytoplasm often dark and coarse (Figs 16, 18, 19).

3. *Good*; supranuclear mosaic pattern of mucosa cells prominent; no cell separations; cytoplasm usually homogeneous and light in color (Fig. 17).

Hindgut inclusion bodies

1. *None*; no inclusion bodies in cytoplasm of mucosa cells (Fig. 20).
2. *Stratified*; most cells with distinct supranuclear zone of relatively pale, coarse material not in the form of discrete spheroid bodies (Fig. 21).
3. *Moderate inclusions*; low to moderate proportion of cells contain one to a few spheroid eosinophilic bodies of small to medium size, *i.e.*, generally smaller than the nucleus (Fig. 22).
4. *Massive inclusions*; large proportion of cells contain one to a few spheroid eosinophilic bodies, often larger than the cell nuclei (Figs 23, 24, 25).

Liver:

Nuclei

1. *Poor*; usually totally black (Fig. 26).
2. *Intermediate*; nuclei with abundant dark granules; nucleoli enlarged or indistinct (Fig. 27).
3. *Good*; nuclei with lightly granular chromatin; nucleoli usually small and distinct (Figs 28, 29, 30, 31, 36).

Cytoplasm

1. *Hyaline*; cytoplasm lacks texture and/or appears dark; cells usually small, often separated (Fig. 26).
2. *Homogeneous*; cytoplasm granular, often with slight variability in coloring (Figs 28, 29).
3. *Variable*; cytoplasm contains numerous eosinophilic granules of various sizes (Figs 30, 36).
4. *Structured*; cytoplasm varies in texture from scattered granules to distinctive eosin patches (Fig. 31).

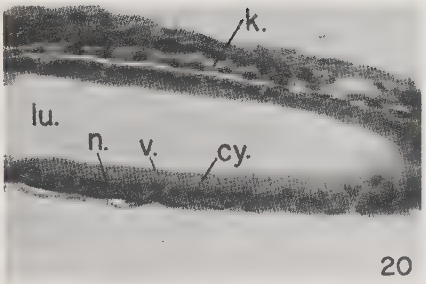
Intracellular space

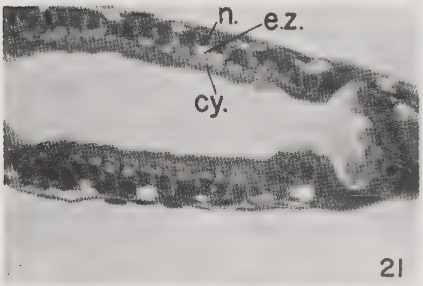
1. *None*; cytoplasm of hepatocytes completely devoid of open gaps; (does not include the highly variable, sometimes large sinusoidal spaces) (Figs 26, 28).
2. *Slight*; occasional small gaps in cytoplasm of hepatocytes, usually scattered (Fig. 29).
3. *Medium*; small gaps in cytoplasm of hepatocytes common throughout the organ (Fig. 30).
4. *Extensive*; gaps in cytoplasm large and present in most hepatocytes, suggestive of vacuolization; boundaries of hepatocytes usually prominent (Figs 31, 36).

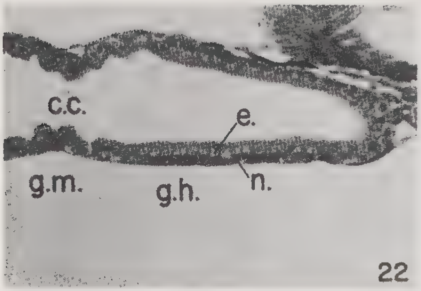
Pancreas:

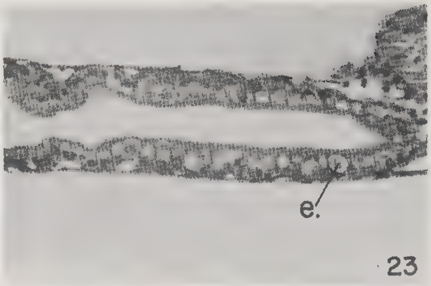
Pancreas proper

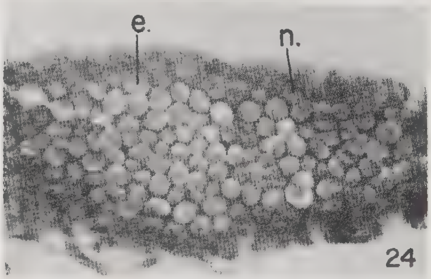
1. *Poor*; cells usually small, black and separating; organ appears thin, with little or no eosin coloration (Figs 26, 32).











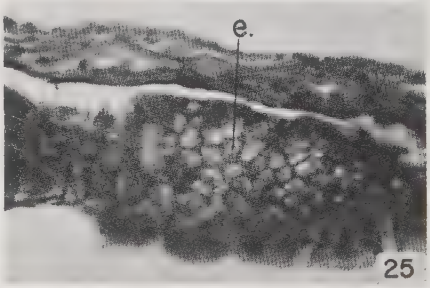


Fig. 20. Hindgut mucosa cells with no eosinophilic inclusions: structure above the hindgut is left kidney duct: 5S-2: ×393.

Fig. 21. Hindgut mucosa showing the stratified condition: eosinophilic material above nuclei light in color and granular and not in form of large spheroid bodies: 3F-2: ×393.

Fig. 22. Hindgut with inclusion bodies of moderate size: these are deeper in color and far more variable in size than previous: constriction in the digestive tube is ileocaecal furrow separating hindgut and midgut: 7F-2: ×250.

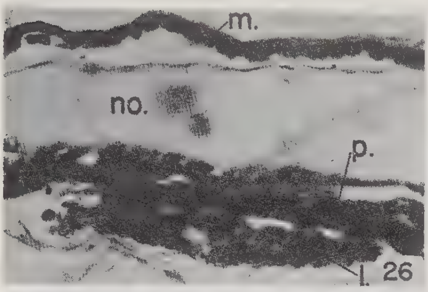
Fig. 23. Hindgut with large eosinophilic inclusion bodies: noticeable variation in size: 7F-3: ×250.

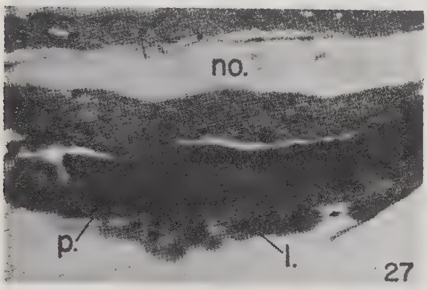
Fig. 24. Hindgut with large spheroid eosinophilic inclusions: size and texture quite uniform: 5F-3: tan: ×393.

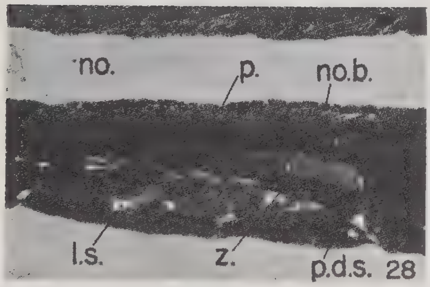
Fig. 25. Hindgut with large spheroid inclusions, but inclusion bodies have coarse, granular texture suggestive of breakdown (intracellular digestion?): 5F-3: tan: ×393.

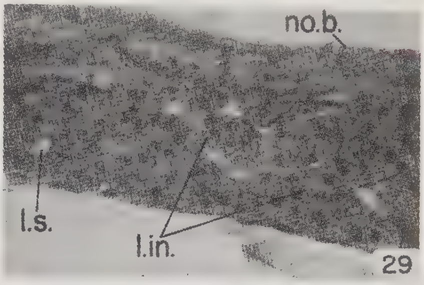
c.c., ileocaecal constriction; cy., cytoplasm; e., eosinophilic inclusion bodies; e.z., supranuclear zone of pale eosin granules; g.h., hindgut; g.m., midgut; k., kidney duct; lu., lumen; n., nucleus; v., microvilli.

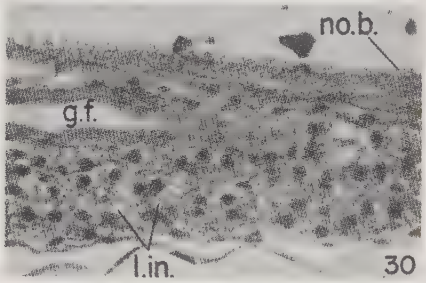
2. *Fair*; at best basophilic chromaffin appears definitely more abundant than eosinophilic zymogen droplets; at worst zymogen negligible with some peripheral cells showing blackness (Figs 27, 33, 34).











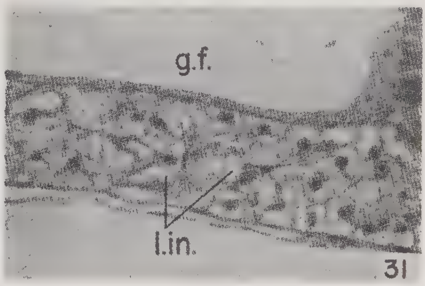


Fig. 26. Liver nuclei poor, cytoplasm hyaline, and intracellular space absent: cells appear to be disintegrating: organ diminished in size and dark: pancreas is also poor, dark, and diminished: 6S-1: ×250.

Fig. 27. Only portion of liver visible showing nuclei in intermediate condition: nuclei contain considerable dark chromatin: pancreas in fair condition, organ is dark but some zymogen throughout: muscle fibers, intermuscular tissue, and notochord shrinkage all intermediate: 6F-2: ×393.

Fig. 28. Liver with good nuclei, homogeneous cytoplasm and no intracellular space: liver sinuses moderate in size: pancreas good though this is not the definitive section for this organ: pancreatic duct sinus filled with fine-textured zymogen: 6F-2: ×250.

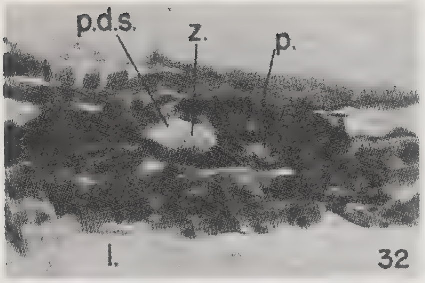
Fig. 29. Liver with good nuclei, cytoplasm showing slightly variable texture and also slight intracellular spaces: 6F-3: ×393.

Fig. 30. Liver with good nuclei, variable cytoplasm and medium intracellular spaces: 6F-3: ×393.

Fig. 31. Liver with good nuclei, structured cytoplasm, and extensive intracellular spaces: 7F-3: ×393.

g.f., foregut; l., liver; l. in., liver intracellular spaces; l.s., liver sinus; m., muscle; no., notochord; no. b., bands of notochord sheath; p., pancreas; p.d.s., pancreatic duct sinus; z., zymogen.

3. *Good*; chromaffin and zymogen appear to be in about equal proportions throughout (Figs 35, 36).
4. *Resting*; zymogen droplets clearly dominant and chromaffin minimal through-



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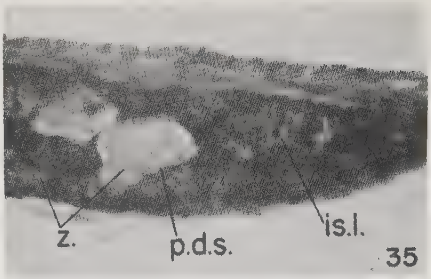

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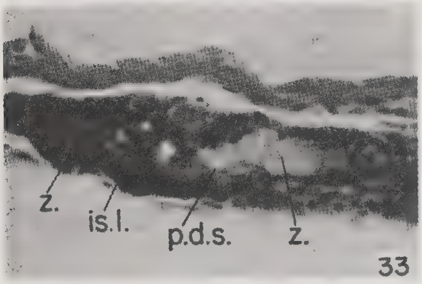

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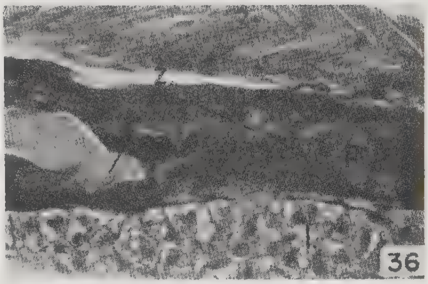
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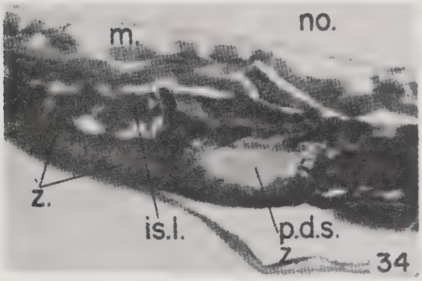

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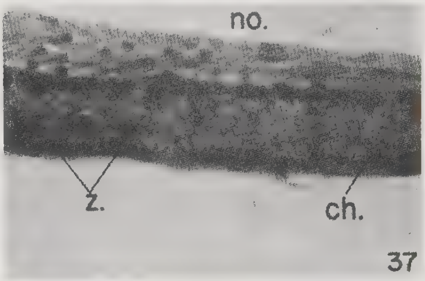

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Fig. 32. Pancreas in poor condition: nuclei pycnotic, cell structure disintegrating: pancreatic duct sinus with a few loose granules of zymogen: little if any zymogen elsewhere in the organ: liver also in poor condition: 6S-1: ×393.

Fig. 33. Pancreas in fair condition: zymogen present but not abundant: nuclei tending towards pycnotic and traces of cell separation: islet of Langerhans composed of contracted cells with pycnotic nuclei: pancreatic duct sinus filled only loosely with zymogen: 5S-1: ×393.

Fig. 34. Pancreas in fair condition: this posterior portion of organ shows cells with zymogen, as in other areas, but also a tendency towards pycnotic nuclei and cell separation in some areas: organ tends to be dark: islet of Langerhans tends to be contracted and pycnotic: duct sinus filled with homogeneous zymogen: typical of many of the day 2 larvae: 2F-1: ×393.

Fig. 35. Posterior portion of pancreas in good condition showing extensive zymogen as well as chromaffin in cells and well expanded duct sinus filled with fine-textured zymogen: note also well expanded islet of Langerhans. 6F-3: ×393.

Fig. 36. Pancreas in good condition showing considerable zymogen but much dispersed chromaffin: duct sinus filled with fine-textured zymogen: liver has good nuclei, variable cytoplasm, and extensive intracellular spaces: 5F-3: ×393.

Fig. 37. Middle region of pancreas in good condition showing peripheral and some dispersed light chromaffin, and extensive complement of zymogen globules in acinar cells: 6F-3: ×393.

ch., chromaffin (basophilia); is. l., Islet of Langerhans; l., liver; m., muscle; no., notochord; p., pancreas; p.d.s., pancreatic duct sinus; z., zymogen.

out (only 12 % of all larvae were given this grade and these were largely day 4 and never beyond day 5).

Pancreatic duct sinus

1. *Empty*; sinus contains no zymogen or only a few scattered granules; sinus usually small and sometimes not visible (Fig. 32).
2. *Partially filled*; zymogen fills most of the sinus but is either very coarse in texture or in separated granules (Fig. 33).
3. *Filled*; zymogen in sinus fine textured or hyaline; sinus always full and relatively large (Figs 28, 34, 35, 36).

The larvae were also graded for the relative quantity and appearance of food in the digestive tract, and for the presence of yolk. Even the largest yolk residues were quite small relative to the hatching larva. Although such information helps to judge the feeding status of a larva, it does not necessarily indicate a state of good health. There were even a few instances where yolk or food was present but in an apparent state of degeneration. Grading was as follows:

Digestive tract contents:

Quantity

1. *None.*
2. *Small to moderate amount*; scattered traces of material or one mass of material occupying a small part of the lumen.
3. *Large amount*; lumen relatively large and at least half filled with material.

Appearance

1. *Debris*; scattered flocculent material, sometimes identifiable as cellular debris associated with atrophy of midgut cells.
2. *Granular*; material granular, loose, pale; often with high chromatophore content.
3. *Mixed*; contents a mixture of granular, fibrous, and membranous elements; chromatophore content low; organism configurations sometimes recognizable.
4. *Membranous*; long membranous elements dominant; usually orientated longitudinally and sometimes densely packed.

Yolk:

1. *Moderate remnant*; small but compact mass, usually teardrop shaped; often surrounded by periblast nuclei.
2. *Trace amount*; one or two small clusters of yolk globules; usually only between bases of pectoral fins; few if any periblast nuclei.
3. *None.*

In addition to the histological characteristics, the lengths of the gall bladder, liver, pancreas, and pancreatic duct sinus were measured. These lengths were, in part, directly related to standard length. Their ratio to standard length did not vary relative to starvation and they were not used in estimating the condition of larvae.

Missing grades. Occasionally it was not possible to grade a given histological characteristic. In some instances the reason was technical, *e.g.*, missing or damaged sections, distorted specimens, *etc.*, but for the most part it was because that particular organ, or the entire larva, was badly disarrayed – had literally come apart in processing – probably because of its frail condition. Since analysis based on the numerical grade data would be complicated by missing values, and since frail condition appeared to be the main reason for missing values, all missing entries were assigned the minimum grade of unity. The effect of this on grade means is small: no one of the 11 histological characteristics included more than 4 % of such assignments. The only extreme cases were three larvae where grades of 1 were assigned for seven or eight of the 11 histological characteristics.

VARIATION BETWEEN AGE-FOOD GROUPS

Fig. 38 shows the mean grade for each of the 11 histological characteristics by age-food group, and in the upper right hand corner for all 11 characteristics averaged: the latter does not include the data for yolk and food in the digestive tract. The number of larvae represented by each age-food group (for all graphs) is as follows:

Age in days	2	3	4	5	6	7	8	9
Fed	15	21	26	18	18	30	8	19
Starved	8	15	15	14	13	1	0	0

In general, average grades for the fed larvae rise over the first few days and remain about the same thereafter, while those for the starved larvae are higher at age 2 days but decline steadily to a low level by age 6 or 7 days. There are some noticeable deviations from this general pattern. Hindgut inclusions, for example, cannot show a decline for the starved group because it starts and remains at the minimum grade, signifying absence of inclusions. While this demonstrates a lack of feeding in contrast to the higher grades for the fed group, it does not necessarily indicate poor health or condition. Many larvae without inclusions during the first few days appeared to be in good condition on the basis of other features. Conversely, the fed group contained individuals at different ages that appeared to be in good condition despite the absence of inclusions, or in poor condition despite the presence of inclusions. In the latter instances the inclusions themselves were oddly colored and misshapen, apparently in a degenerating state.

Another notable feature in the figure for hindgut inclusions is the rise in grade for fed larvae between days 2 and 5. This would seem to indicate increasing hindgut activity following the initiation of feeding, but it may also reflect a change from *Gymnodinium* to *Brachionus* as the main food. While the higher grades, prevalent in later days, undoubtedly represent digestion of *Brachionus* in the hindgut, the rather different stratified condition represented by Grade 2 and prevalent during the first few days, may be a histological expression of *Gymnodinium* digestion. The contents of the

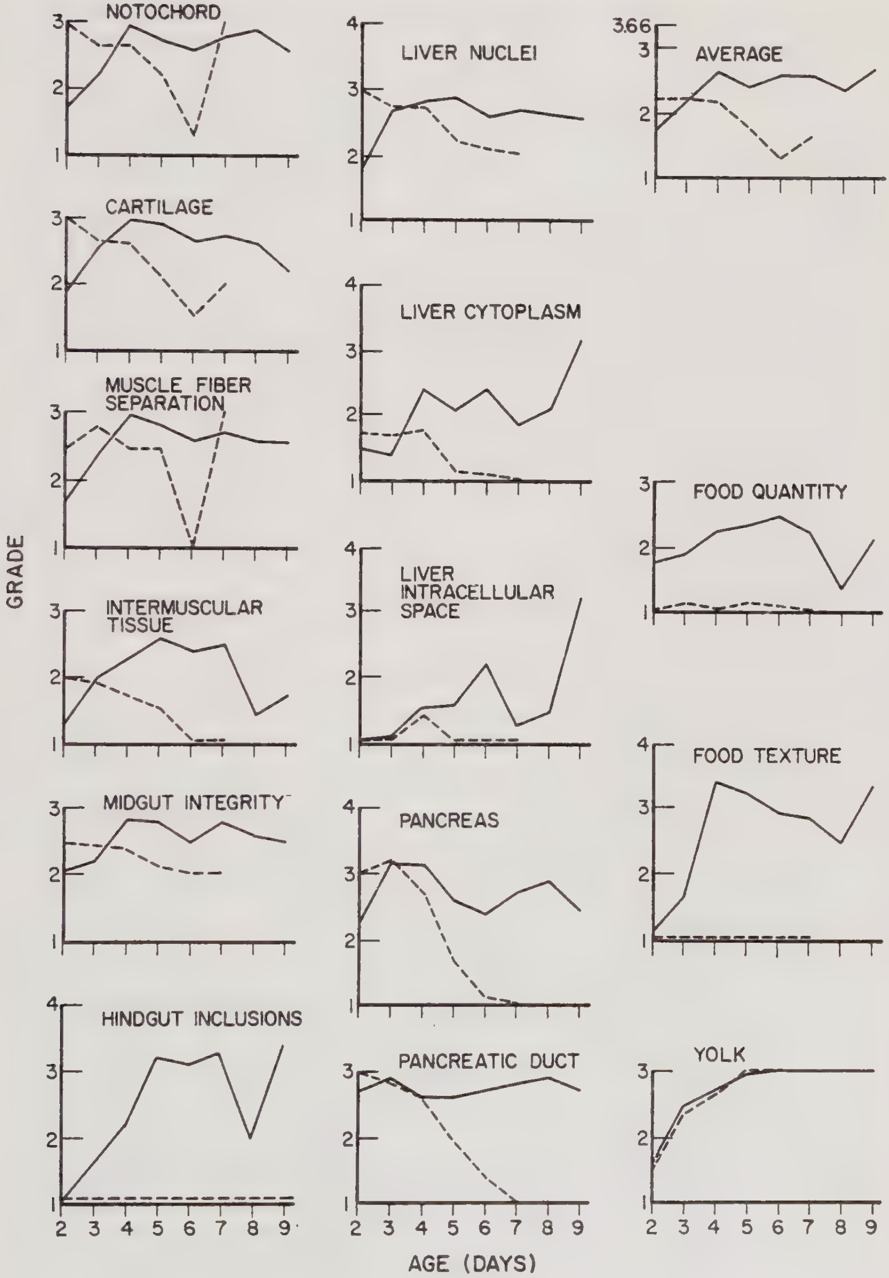

Fig. 38. Relation between average grade and age for fed (solid lines) and starved (dashed lines) larvae for each of the 11 histological features, and for food texture, quantity, and yolk: upper right, average for all histological features: highest grade, healthiest condition: for yolk highest grade, complete absence: see p. 302 for number of larvae.

digestive tracts of larvae showing the stratified state contained an abundance of light greenish granules, probably chromatophores of *Gymnodinium*. Some older larvae were also graded 2 for the hindgut, but re-examination showed that in these instances the condition was one of large inclusions composed of loose granules, which may represent a breakdown phase in the hindgut digestion of *Brachionus*. Despite these uncertainties with regard to the interpretation of hindgut grades, the pattern of averages shows that this characteristic is at least relevant as an indicator of recent feeding status of the larva.

Liver intracellular space is the only other histological characteristic giving minimum average grades for both fed and starved larvae at age 2 days and, with one small exception, for starved larvae throughout. Another deviation in this pattern is the sharp rise to a high grade at age 9 days for fed larvae following a more or less gradual rise through the earlier ages. This probably indicates low but increasing stores of energy reserves (glycogen?) in hepatocytes of fed larvae culminating in abundant large vacuoles with appreciably greater stores, as compared with the absence of stored reserves in hepatocytes of starved larvae. The characteristic indicates differences contingent on the availability of food and is pertinent to health or condition; even so it must be noted that the pattern of grades, like that for hindgut inclusions, differs from those for other characteristics in not showing an appreciable decline in the starved larvae.

In certain respects, the pattern for liver cytoplasm resembles that for liver intracellular space including a high average grade for 9-day-old larvae; this is because the two characteristics are to some extent interdependent. The nature of the variation in liver cytoplasm and the criteria for grading it were, however, such that this characteristic does show a definite element of decline for starved larvae and of increase for fed larvae.

Muscle fiber separation and notochord shrinkage each contain a peculiarity in their high grade for 7-day-old starved larvae. These values indicate no separation or shrinkage, phenomena that were increasingly apparent in starved larvae over the preceding few days. Day 7 is, however, represented by only one specimen at a time when most larvae without food had already died, and it appears that this one may have reached a degree of emaciation not anticipated in the grading criteria for muscle and notochord. (My notes on this specimen contained the observation that although muscle fibers did not show separations, they were thin and the organelle structure seemed degenerate. Thus, it seems possible that the fibers had gone through a separation stage but had finally shrunken to secondarily eliminate spaces, including those around an already shrunken notochord.) It may be seen that all other characteristics of this specimen were graded low, and that the high values for muscle and notochord do not appreciably raise the average for all 11 characteristics at the day 7 starved point.

The above mentioned deviations notwithstanding, it is evident that the patterns of grades for the histological characteristics tend to parallel the trends in the survival and length, and that the grading scales are, therefore, good indices of the effects of starvation on the larvae. This is especially true for the pattern of averages based on all 11 characteristics, indicating that such averages will provide the best index of condition. The pattern for pooled grades shows that values approximating unity are primarily associated with the greatest mortality in the starved series and reflect severe emaciation, while values approaching three are associated with good survival in the fed series and reflect, therefore, the robust condition. Values approximating to two are primarily associated with the starved series, especially with the few days just preceding total mortality from starvation, and may be considered to represent moderate emaciation. There is an anomaly at age 2 days in that fed larvae had relatively low grades at a time when yolk remnants were still present and adverse effects from food deprivation would not be expected. This will be discussed below.

VARIATION WITHIN AGE-FOOD GROUPS

When grades for the 11 histological variables are averaged for a single larva the lowest possible score is 1.00 and the highest score 3.36. When this range is divided into three equal classes, the class intervals are 1.00 to 1.78, 1.79 to 2.56, and 2.57 to 3.36. In view of the preceding section, these classes may be considered to represent severe emaciation, moderate emaciation, and the robust condition, respectively. The percentage distributions of larvae by average grades among these three classes (Fig. 39) show that the composition of the age-food groups vary in a way that is consistent with the survival and length patterns for fed and starved larvae. In the fed series larvae are equally divided between the moderate emaciation and robust classes at age 4 days, but beyond this age the majority are in the robust class. In the starved series, the majority are initially in the moderate emaciation class but the proportion in this class decreases, while the proportion in the severe emaciation class increases to 100 % at ages 6 and 7 days, as mortality also increases and eventually becomes total.

The presence of some larvae in the two emaciated classes in almost every age group is not inconsistent with the survival and length data. There was some mortality in all groups, and average length was lower than expected in the day 8 and especially the day 9 groups, both of which had relatively high proportions of moderately and severely emaciated larvae. The interesting point with regard to length at ages 8 and 9 is that poor condition probably indicates suboptimal growth for an identifiable portion of the sample. Why severely and moderately emaciated larvae occur in the fed groups is not known, but it would appear that unavailability of food is not always the underlying cause of declining condition.

On the other hand, the high proportion of severely emaciated larvae in the 2-day-old group of the fed series is not easily reconciled with the circumstances of the experiment. Starvation should not have been a danger. Many of the larvae still had vestiges of yolk and *Gymnodinium*, known to be an adequate food for early feeding of the anchovy (Lasker *et al.*, 1970) was available; however, the hindguts showed no evidence of intracellular digestion and the midguts were either empty or contained only small amounts of material regarded as debris. The debris may have been the residue of ingested *Gymnodinium*, but in some instances at least, it was the residue of disintegrating, atrophied midgut cells. Atrophied cells, though more prevalent in the 3-day-old fed group, were identifiable in some of these day 2 specimens. They are mucosa cells which become spherical and pass into the lumen before disintegrating. The process is probably an aspect of tissue retrenchment. The poor condition shown by most of the larvae of this group could also have been a behavioral phenomenon. If success were low in early attempts to capture food, perhaps because of a brief learning period and/or because food density was low, the larva might have incurred an energy deficit accompanied by symptoms of emaciation. Two-day old larvae with no food available, on the other hand, might have remained in somewhat better condition because they were not stimulated to expend energy in attempting to capture food.

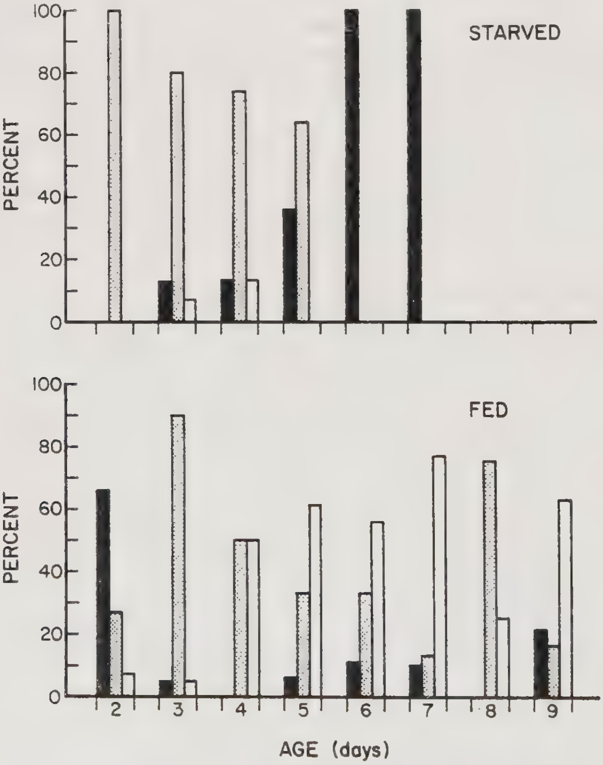

Fig. 39. Percentage of larvae in each of three classes, severe emaciation (dark), moderate emaciation (gray), and robust (white) for each age group in fed and starved series: the three classes represent equal intervals of the range of average grade for a single larva, where the average is based on grades for all 11 histological features pooled: no. of larvae, see p. 302.

Whatever the reason for the relatively poor condition of most of the 2-day old larvae, the pancreas differed in an interesting way from that of larvae in the severely emaciated class after 5 or 6 days of starvation. The latter had low grades for both the pancreas proper and the pancreatic duct, indicating that they were not synthesizing digestive enzymes and that the duct sinus contained little, if any, reserve for immediate digestive activity. By contrast, despite the low and intermediate grades for the pancreas proper, almost all of the 2-day old fed larvae had high grades for the pancreatic duct, which was well expanded and filled with homogeneous zymogen. It is possible that many of these larvae, though considerably emaciated, were still capable of immediate digestive activity.

Apart from the special problem with 2-day old larvae, the general compatibility of the distribution of average grades within the age-food groups with survival and length demonstrates that the condition of individual anchovy larvae may be evaluated from histological parameters independent of age or size for the range studied, regardless of the factors producing the condition. On the same grounds, it appears that the three class intervals used to describe the distribution of average grade may be considered to approximate severe emaciation that is irreversible, moderate emaciation that is reversible, and robust health.

ORDER OF IMPORTANCE OF HISTOLOGICAL CHARACTERISTICS

To determine how many of the 11 histological variables would be required to establish the condition of the larva, and also the relative importance of the variables the data were submitted to a stepwise discriminant analysis (Dixon, 1965). The analysis assembles variables in the order by which they reduce the ratio of within to total generalized variances among predetermined groups into which the items are being classified (Rao, 1952). The items are larvae, each with an average grade for all variables that identifies it as belonging to one of three pre-determined groups, severely emaciated, moderately emaciated, or robust, which were defined as specific intervals of

TABLE I

Order of selection of histological variables by discriminant analysis for four age arrays: lower half is repeat of analysis with variable HG excluded. C, cartilage; HG, hindgut inclusions; IM, intermuscular tissue; Lc, liver cytoplasm; Ln, liver nuclei; Ls, liver intracellular space; M, muscle fiber separation; MG, midgut integrity; NO, notochord shrinkage; P, pancreas condition; PD, pancreatic duct sinus.

Age in days	No. of larvae	Selection steps										
		1	2	3	4	5	6	7	8	9	10	11
All variables												
5–9	121	P	M	IM	HG	NO	Lc	C	PD	Ln	MG	Ls
4–9	162	P	M	HG	IM	C	Ls	PD	NO	MG	Lc	Ln
3–9	198	M	HG	P	IM	C	Lc	MG	PD	NO	Ls	Ln
2–9	220	M	HG	P	IM	C	Ls	MG	NO	PD	Lc	Ln
Variable HG excluded												
5–9	121	P	M	IM	Lc	NO	PD	MG	C	Ln	Ls	—
4–9	162	P	M	IM	Lc	NO	PD	MG	C	Ln	Ls	—
3–9	198	P	NO	IM	Lc	M	PD	MG	C	Ln	Ls	—
2–9	220	P	NO	IM	Lc	Ln	M	PD	C	MG	Ls	—

average grade. For the present purpose, the percentage of larvae that are correctly placed in the predetermined groups as each variable is added is taken as an indication of the improvement in discrimination. The first variable selected, of course, is the one that effects the greatest reduction in variance when the variables are compared individually.

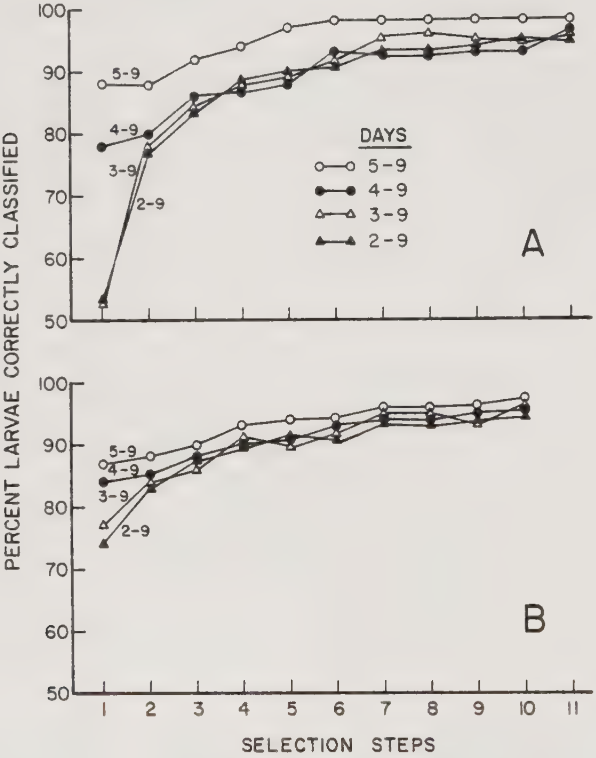

Fig. 40. Percentage of larvae correctly identified (as severely emaciated, moderately emaciated, or robust) in relation to the successive addition of histological variables in stepwise discriminant analysis: 'correct' class for a larva based on its average grade for all the histological variables: see text and Table I for further details: A, all 11 histological variables included in analyses: B, the variable, hindgut inclusion bodies (HG), not included in analysis.

The discriminant analysis was run on eight different arrays of larvae, namely, days 5 to 9 inclusive (*i.e.*, encompassing all larvae from both the fed and starved series for these days and without regard to age or food treatment) days 4 to 9, days 3 to 9, and days 2 to 9, and the same sets repeated but with one of the variables, hindgut inclusions, not included. The last of these arrays includes all the larvae studied, while the first includes larvae for the age span when histological differences between the fed and starved groups were distinct. The order in which variables were selected for each array is shown in Table I, and the percentage of larvae correctly classified (into the three classes) as each variable was added in Fig. 40.

In the arrays where all 11 variables were used, the same four features rank at the top but their order changes as younger larvae are included. Pancreas condition (P) falls to third place while muscle fiber separation (M) and especially hindgut inclusions (HG) advance; however, the percentage correctly classified also declines with these changes. Thus, where the youngest larvae are included along with all others, muscle fiber separation (M) yields the best discrimination for classification on the basis of a single feature, but this discrimination is not nearly so good as that shown by pancreas condition (P) where only the 5 to 9-day old larvae are involved. On the other hand, discrimination is quite high for the arrays including the 2 and 3-day old larvae if it is based on four or five histological features. Approximately 90 % of all larvae are then correctly classified as severely emaciated, moderately emaciated, or robust. For the array of 5 to 9-day old larvae correct classisfication is equally good on the basis of the pancreas condition (P) alone.

The arrays were rerun with all information on hindgut removed because it ranked high in the order of selection given above and yet had previously been described as an indicator of feeding or non-feeding but not necessarily a reliable indicator of the state of emaciation of the larva; in the youngest larvae making their first attempts at feeding, for example, even the most robust individuals are not likely to have large inclusion bodies in the hindgut. At best, they might show the stratified condition, which recieved a low grade. Elimination of the hindgut feature from the average score for all variables slightly changed the intervals defining the severely emaciated, moderately emaciated, and robust classes. The class intervals now become 1.00 to 1.76, 1.77 to 2.53, and 2.54 to 3.30. There were also changes in the distribution of larvae among the three classes, amounting to 2 % for the 5 to 9, 5 % for the 4 to 9, and 9 % for the 3 to 9 and 2 to 9-day old arrays. These were almost entirely due to transfer of larvae from the moderate emaciation to the robust class. They do not alter the essential compatibility of the distribution of histological grades with the survival pattern.

With hindgut eliminated, pancreas condition (P) occupies the position of first importance for all the arrays. Muscle fiber separation (M) is replaced in second position by notochord shrinkage (NO) when the arrays include 3 and 2-day old larvae, but intermuscular tissue (IM) and liver cytoplasm (Lc) occupy the third and fourth positions respectively for all arrays. Fig. 40 shows, moreover, that with hindgut removed, the first variable, *i.e.*, pancreas condition (P), produces a relatively high percentage of correct classifications for the arrays containing the youngest larvae. Nevertheless, correct classification does not exceed 90 % until the evaluation is based on four variables. Little is gained by the addition of more variables.

From the foregoing considerations it may be stated that the condition of the anchovy larva can be evaluated with confidence on a histological grading scale that does not include the status of the hindgut inclusions, but does include pancreas condition and at least three other features, preferably muscle fiber separation, intermuscular tissue, and liver cytoplasm. Substitutions could be made for any of these last three, if necessary, from among the variables that were placed lower in the order of selection without seriously compromising an evaluation. All of them had significant *F* ratios (likelihood ratio tests) when tested for inclusion, so that each variable still showed some capacity for discriminating larvae of the three classes, given the variables already entered.

DISCUSSION

These results on the anchovy are similar in many ways to those obtained by Umeda & Ochiai (1975) on the yellowtail. In both cases food deprivation results in signs of degeneration of the cells in the intestine, the pancreas, and liver, and the degeneration tends to become more severe with starvation. The availability of food, on the other hand, tended to promote production and storage activities of cells and tissues. For the anchovy, additional signs of decline were evident in cell shrinkage, separation, and the loss of intercellular substance, particularly in the trunk musculature and cartilage elements. The presence or absence of eosinophilic inclusion bodies in the hindgut is, in both species, strongly associated with the availability and non-availability of food respectively. In both studies, three classes of larvae were defined. For the yellowtail these were starved, semi-starved, and feeding, and among larvae provided with food the semi-starved group was distinguished from the feeding group only by its lack of eosinophilic inclusions in the hindgut cells and lack of food in the lumen of the digestive tract. Umeda & Ochiai concluded that larvae in this condition would have the ability to absorb and digest food if it were to become available. They recognized, on the other hand, that even with food available some of the larvae weakened and, for unknown reasons, died as was also the case with the anchovy. For the anchovy the three classes, severe emaciation, conditional emaciation, and robust were based on several histological characteristics. Hindgut inclusions ranked high in discriminating among the classes but this was considered to be more an indication of feeding status in the particular circumstances of the experiment than of condition or health. Discrimination of the three classes was actually improved if hindgut was excluded from consideration. In samples of sea-caught larvae the characteristic should no doubt be taken into consideration but interpreted with caution. The absence of inclusions, for example, might be a regular feature of the daily feeding cycle, but in some instances their absence might be a sign of low food availability with the threat of emaciation and reduced probability of survival. Not enough is yet known about the dynamics of intracellular digestion in the hindgut.

Another circumstance suggesting a need for special consideration is the relatively poor condition of 2-day old fed larvae and the fact that the inclusion of these larvae diminished the adequacy of the discrimination analysis. This indicates that grades for some of the characteristics do not reflect the average grade based on all characteristics as well in the 2-day old group as in the older age groups, where grades, moreover, were better related to the survival pattern. One reason for the lack of consistency in grades might have been the relatively high grades for the pancreas and especially for the pancreatic duct sinus in the otherwise emaciated 2-day-old larvae. This suggests that at this age they retain a ready reserve of zymogen which gives them a capacity for immediate digestive activity and rapid recovery if food were encountered. If so, signs of emaciation have less import as an indication of imminent mortality from starvation at 2 days of age than they do at 4 to 6 days of age. In view of the uncertainties, larvae from sea samples suspected of being 1 or 2 days old, perhaps on the basis of yolk remnants, should probably be treated as a special group or disregarded in making estimates of condition.

Although there are some points of ambiguity, it has been demonstrated that at least for anchovy larvae at and just beyond yolk absorption, signs of emaciation are a cumulative function of starvation, and that they may be expressed as a numerical index of condition or health. For the experimental material the numerical index varied with survival, from which it is inferred that degree of emaciation indicates the probability of survival. Where minimum and maximum possible grades are assumed to represent zero and 100 % survival potential respectively, experimental larvae categorized as moderately emaciated would have survival potentials ranging between 33 and 66 %. Such ratings, whether based on the foregoing variables or on some modified or different numerical coding, may undoubtedly be determined for larvae taken from the ocean. While such values might not be direct estimators of survival of larvae, they should at least be useful measures of the starvation parameter for multifactor estimates of survival.

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7637

FIRST RECORD OF THE MELON-HEADED WHALE, *PEPONOCEPHALA ELECTRA*, IN THE EASTERN PACIFIC, WITH A SUMMARY OF WORLD DISTRIBUTION

Peponocephala electra (Gray 1846) is a tropical pelagic delphinid previously known to occur in the eastern Atlantic, Indian, and western and central Pacific oceans. It is also known as the electra dolphin, the Hawaiian blackfish, and the many-toothed blackfish. Since van Bree and Cadenat (1968; localities 1-4, 6-9, 11, 13, 14, 16, 18, and 19 in Figure 1) summarized world records, the species has been reported from Thailand (Pilleri 1973, locality 17), the Philippine Sea near Cebu (W. H. Dawbin pers. commun., locality 15), near Townsville, Australia (G. E. Heinsohn pers. commun., locality 12), the New Hebrides (Rancurel 1974, locality 10), and the Tuamotos-Marquesas region (K. S. Norris pers. commun., locality 5). Records cited by van Bree and Cadenat (1968) as "in litteris" or in press, have subsequently been published (Dawbin et al. 1970, locality 11; Mörzer Bruyns 1971, localities 6-9). The purpose of this note is to report a capture that extends the known range of the species some 3,000 miles into the eastern tropical Pacific off Central America (Figure 1; triangle).

The specimen (Figure 2), a male calf 112 cm long (tip of upper jaw to base of notch in flukes) and weighing 15 kg, was captured in a tuna purse seine that had been set on an aggregation of yellowfin tuna, *Thunnus albacares*, and dolphins, *Stenella* sp., approximately 90 nautical miles (about 167 km) due west of Champerico, Guatemala (lat. 14°20′N, long. 91°52′W), in May 1974. More precise information on date and locality of capture is not available. A crew member found the calf dead in the net, placed it in the ship's freezer, and on return to port donated it to the National Marine Fisheries Service, La Jolla. The specimen was identified using X rays of the dentition. The high tooth count $\left(\frac{23+ \mid 23+}{22+ \mid 22+}\right)$, combined with the blunt head and dark coloration, is diagnostic of the species. The specimen was then photographed, measured, weighed, cast in plastic, and sent frozen to the U.S. National Museum (USNM), Washington, D.C., where it was preserved whole

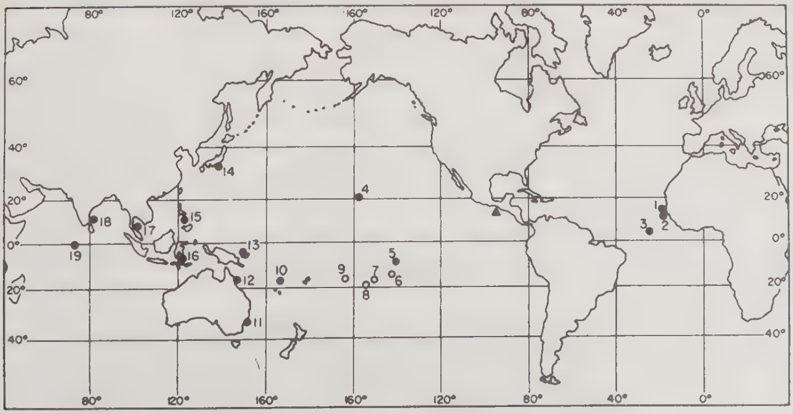

FIGURE 1. — Known distribution of *Peponocephala electra*. Triangle is new record; sources of others in text. Closed circles are specimen localities, open circles are sightings. Some circles represent multiple records from single localities, e.g., Hawaii and Honshu, Japan.

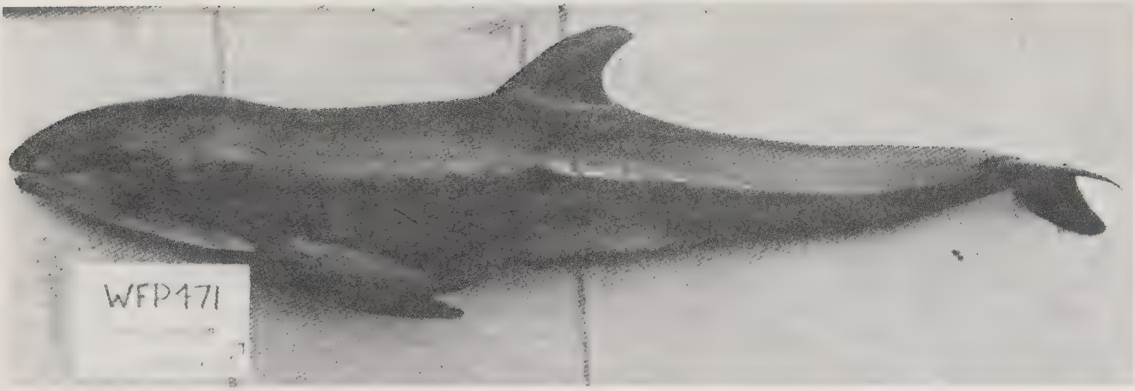

FIGURE 2. — Calf of *Peponocephala electra* collected in eastern tropical Pacific (USNM 504087).

and placed in the marine mammal collection (USNM 504087).

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FOODS OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, IN THE INSHORE COASTAL WATERS OF BRISTOL BAY, ALASKA, 1966-67

For most living organisms the early portion of life is most critical in determining survival. Anadromous fishes such as Pacific salmon have two critical periods during early life — development and growth in fresh water and subsequent adaptation to a marine environment. The food of juvenile salmon during the first few months of marine life influences growth and condition, which in turn probably influences parasitism, predation, and other factors which ultimately determine marine survival.

Although the sockeye salmon, *Oncorhynchus nerka* (Walbaum), is one of the most valuable commercial fishes in Alaska and has been the object of extensive research, little is known of its early life in the sea. Straty (1974) and Straty and Jaenicke[1] have made the only comprehensive study of early marine life of the sockeye salmon in Bristol Bay, historically the largest sockeye fishery in the North Pacific. Documented studies of sockeye salmon food habits during this period of life are generally limited to brief accounts of Soviet research in Kamchatka waters (Synkova 1951), a study in British Columbia (Manzer 1969), examination of a few specimens from Aleutian and Kodiak waters (Chamberlain 1907), and 45 specimens taken off Cape Seniavin in lower

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[1] Straty, R. R., and H. W. Jaenicke. 1971. Studies of the estuarine and early marine life history of sockeye salmon in Bristol Bay, 1965-67. Unpubl. manuscr., 137 p. Northwest Fish. Cent. Auke Bay Lab., Natl. Mar. Fish. Serv., NOAA, Auke Bay, AK 99821.

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GROWTH AND REPRODUCTION OF THE SPOTTED PORPOISE, *STENELLA ATTENUATA*, IN THE OFFSHORE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, JAMES M. COE, AND JAMES R. ZWEIFEL[1]

ABSTRACT

This study is based on data from several thousand specimens of spotted porpoise, *Stenella attenuata*, incidentally killed in the purse seine fishery for yellowfin tuna, *Thunnus albacares*. Average length at birth is 82.5 cm. Gestation is 11.5 mo. Average length at 1 yr is 138 cm. Length-weight equations are given for fetuses and postnatal males and females. Age was estimated from dentinal layers in thin sections of teeth. A two-phase Laird-Gompertz growth model was fitted to the layer-length data. Direct calibration of the dentinal layers beyond the first year (two layers) was not possible, and three alternative hypotheses were considered: 1) two layers per year, until pulp cavity occluded, 2) two layers per year in first year, and one per year thereafter, and 3) two layers per year until puberty, and one per year thereafter. The second alternative is most probably the correct one, but reproductive parameters were estimated in terms of layers. Breeding is diffusely seasonal, with prolonged calving seasons in spring and fall and a pronounced low in winter. A third calving season may exist in the summer. Average age at attainment of sexual maturity of males is approximately 12 layers (average length about 195 cm and average weight about 75 kg). Females attain sexual maturity on the average at about 9 layers and 181 cm. Ovarian changes in adult females are described. Apparently postreproductive females were encountered in the samples. It is concluded that corpora albicantia of ovulation and pregnancy persist indefinitely in the ovaries. It was not possible to distinguish between the two types of corpora. Ovulation rate changes with age, from about four per layer in very young adult females, to about one per layer in older females. The average calving interval is 26 mo long and consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus. About 9.6% of lactating females are also pregnant. Pregnancy rate decreases with age, from about 0.6 per year at 8 to 10 layers, to about 0.3 at 16 layers. The overall sample contained 44.9% males and 55.1% females. Sex ratio changes with age, from near parity at birth, indicating higher mortality rates for males. Gross annual production of calves, based on age and sex structures of the sample and the estimated pregnancy rate, is 14.4% of the population per year. No evidence was found of age or sex segregation in schooling. The estimated parameters differ in a consistent way from those estimated for a population of *Stenella attenuata* in the western Pacific, possibly reflecting the exploitation in the eastern Pacific.

Porpoises of the genera *Stenella* and *Delphinus* are killed incidentally in the tuna seine fishery in the eastern tropical Pacific (Perrin 1969, 1970a; National Oceanic and Atmospheric Administration[2]). Since 1968, the National Marine Fisheries Service (NMFS) has conducted a program of research into the population biology of the major porpoise species to assess the impact of this fishing mortality on the porpoise stocks. The purpose of this paper is to describe the life history of the spotted porpoise, *Stenella attenuata* (Gray),[3] the animal most frequently killed in the fishery.

Little information on life history of the spotted porpoise has been available until very recently. Harrison et al. (1972) examined the gonads of 6 specimens from Japan (5 males and 1 female) and 45 specimens of *S. attenuata* from the eastern tropical Pacific (19 males and 26 females), but did not separate their results and conclusions from

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[1] Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92039.

[2] National Oceanic and Atmospheric Administration. 1972. Report of the NOAA Tuna-Porpoise Review Committee, September 8, 1972. Unpubl. rep. U.S. Dep. Commer., Wash., D.C., 63 p.

[3] The taxonomy of the spotted porpoise has long been confused. Recent morphological studies (Perrin in press) have shown that the spotted porpoise in the tuna fishery is conspecific with the spotted porpoise occurring around Hawaii. The name *S. attenuata* (Gray 1846, holotype from unknown locality) applied by True (1903) to the Hawaiian form is used here for the eastern Pacific form, taking priority over *S. graffmani* (Lönnberg 1934). This usage is strictly provisional, pending the completion of current taxonomic studies, when a different name, such as *S. dubia* (G. Cuvier 1812) or *S. frontalis* (G. Cuvier 1829) may take priority.

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those for *S. longirostris*. Preliminary unpublished results of our studies indicate that these two species are probably disparate in such growth parameters as length at birth, length at maturity, and asymptotic length. Harrison et al. (1972) stated that lengths of the fetuses examined indicate that parturition occurs both in the spring and in the autumn. They described in detail the gross and microscopic histological appearances of several pairs of ovaries. A maximum of nine corpora albicantia were encountered. They concluded that if all the corpora albicantia in ovaries of specimens of this species do not represent past pregnancies, either the fertility is very low or the corpora are not permanent.

Nishiwaki et al. (1965) published length-frequency distributions of 34 fetuses (up to 106 cm long) and 194 postnatal animals (104 to 208 cm) from a school driven ashore in Japan. They estimated that gestation lasts 1 yr, length at birth is about 105 cm, juveniles reach 150 cm in 6 mo, and adult size (180 cm for females and 190 cm for males) is reached in 1 yr. They concluded that there are two seasons for mating and parturition, in the spring and in the autumn, and that there are fewer males than females among adults. Ontogenetic changes in coloration, external proportions, organ weights, the skeleton, parasite load, and feeding habits have been described (Perrin 1970b, in press; Perrin and Roberts 1972; Dailey and Perrin 1973; Perrin et al. 1973).

Kasuya et al. (1974) recently published results of a study of several hundred specimens caught in the Japanese fishery for *S. attenuata*. Their results are discussed and compared with ours in the body of this paper.

METHODS AND MATERIALS

Observer Program

Beginning in 1968, NMFS placed observers aboard U.S. tuna seiners to collect information on the incidental take of cetaceans in the eastern tropical Pacific. Observers were placed on 1 cruise in 1968, 5 in 1971, 12 in 1972, and 22 in 1973. Most of the cruises were 30 to 60 days long. In addition, biological data were collected during chartered cruises of commercial seiners: one in 1971, one in 1972, and two in 1973.

The data collecting had to be carried out in such a way as to not interfere with the fishing operation. Hence, the amount of information collected on the animals killed in a net set varied widely, depending on the amount of time that was available before the next set was made. Following is the hierarchy of types of data that were collected (sample sizes were largest for the first and smallest for the last):

Animals killed were:

1. Counted (estimates were made in cases where counts were not possible), usually on the deck or in the net,
2. Identified to species (and race when possible),
3. (*S. attenuata* only) identified to developmental color pattern phase (Perrin 1970b), and sexed,
4. Measured (to nearest centimeter with 2-m calipers), and
5. Dissected to collect information on reproductive condition (for females, mammaries were examined and reproductive tract collected; for males, the right testis was collected) and age (a section of the left lower jaw at midlength was collected). The gonadal material and jaw sections were preserved in 10% Formalin.[4] Small fetuses (≤ 30 cm) were preserved in the uterus. Larger fetuses were removed from the uterus and frozen.

For each specimen that was at least measured (step 4 above), a field serial number was assigned, and a specimen data sheet was filled out. Data for specimens that were not at least measured were collected on a running tally.

The Study Area

One of us has described the distribution of *S. attenuata* in the eastern tropical Pacific (Perrin 1975). The known occurrence of mixed aggregations of cetaceans and tuna is strongly correlated with certain oceanographic conditions peculiar to that region. The porpoise-tuna association is known only in the eastern tropical portion of the Pacific. That area, which has been called the North Pacific Equatorial water mass (Seckel 1972), has an unusual oxygen-salinity-temperature structure. The reason for this is not fully understood but certainly has to do with the latitude of the area, its position relative to the rest of the Pacific and to the American continents, and the shapes of the adjacent land masses. These factors interact with general global oceanic and atmospheric circulation to produce a water mass with relatively high surface temperature, low surface salinity, a strongly developed, shallow thermocline (usually within 100 m of the surface), and a pronounced, thick oxygen minimum layer just below the thermocline. The effect is to create a very extensive but shallow warm habitat with a sharp oxythermal floor. To the west, these conditions tail off along a divergence centered on lat. 10°N (Wyrtki 1964). The conditions must be causally interrelated, but one of the more striking correlations with the occurence of the mixed-species aggregation is in the thickness of the oxygen minimum layer (Figure 1).

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The occurrence of the aggregation is not tightly correlated with the geographic distributions of the major prey species of the participating predators. Major shared prey items are the ommastrephid squid *Dosidicus gigas,* an unidentified ommastrephid (probably *Symplectoteuthis* sp.), a scombrid fish *Auxis* sp. (*A. thazard* or *A. rochei*), and the exocoetid fish *Oxyporhamphus micropterus* (Perrin et al. 1973). *Dosidicus gigas* is primarily equatorial but migrates sporadically as far as California and southern Chile, far beyond the limits of the distribution of the mixed-species aggregation (Clarke 1966; Young 1972). Species of *Symplectoteuthis* occur widely in the tropical Pacific and Indian oceans (Clarke 1966). *Auxis thazard* occurs in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans," and *A. rochei* in "tropical and subtropical waters of the Indo-Pacific and Atlantic oceans, including the Mediterranean Sea" (Richards and Klawe 1972). The genus *Oxyporhamphus* is also pantropical (Bruun 1935). At least some of the several myctophid fishes in the aggregate apparently are a mainstay of the diet of the spinner porpoise in mixed schools (Perrin et al. 1973) and are not restricted to the tropics but occur also in temperate waters of the eastern Pacific (Moser and Ahlstrom 1970) and elsewhere. These facts, combined with the pantropical distributions of the cetaceans, tunas, and birds, suggest that the multispecies aggregation does not have its roots in the distribution of the component species or their prey but rather in the peculiarities of the physical oceanography of the region.

The Sample

In 1971 and early 1972, when more specimens were decked than could be processed in the time available (the limit per net set was usually about 35 to 40 specimens), adult females were selected for measuring and dissection. The intention was to insure that sample sizes would be large enough to allow estimation of pregnancy rate with adequate precision. The information on age structure of the catch for that period is limited to the coloration phase data. The observer program subsequently expanded, and beginning in October 1972 no selection was practiced in determining which animals were to be dissected; the first 35 to 40 specimens of both sexes and all ages that came to hand were set aside for measuring and dissection and the remainder discarded. The length data for 1968 and for October 1972-December 1973 are presumably cross-sectional with respect to the kill.

The sample of animals at least measured included 3,504 postnatal animals and associated fetuses from known localities and 23 from imprecisely known localities (Figure 2). Coloration phase and sex data were collected for another 6,150 specimens. In addition, some data were available for 45 other specimens collected by other research agencies, museums, and private individuals. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1).

Two races of *S. attenuata* exist in the eastern tropical Pacific — a large coastal form and a small offshore form (Perrin 1975, in press). This paper deals only with the offshore form. The estimates of life history parameters cannot be assumed to apply also to the coastal form.

TABLE 1.—Samples of postnatal spotted porpoise by month for all years.

Month	Males	Females	Total
January	748	443	1,191
February	263	209	472
March	298	147	445
April	216	155	371
May	181	97	278
June	69	58	127
July	1	0	1
August	6	5	11
September	0	0	0
October	222	158	380
November	110	87	197
December	30	24	54
Total	2,144	1,383	3,527

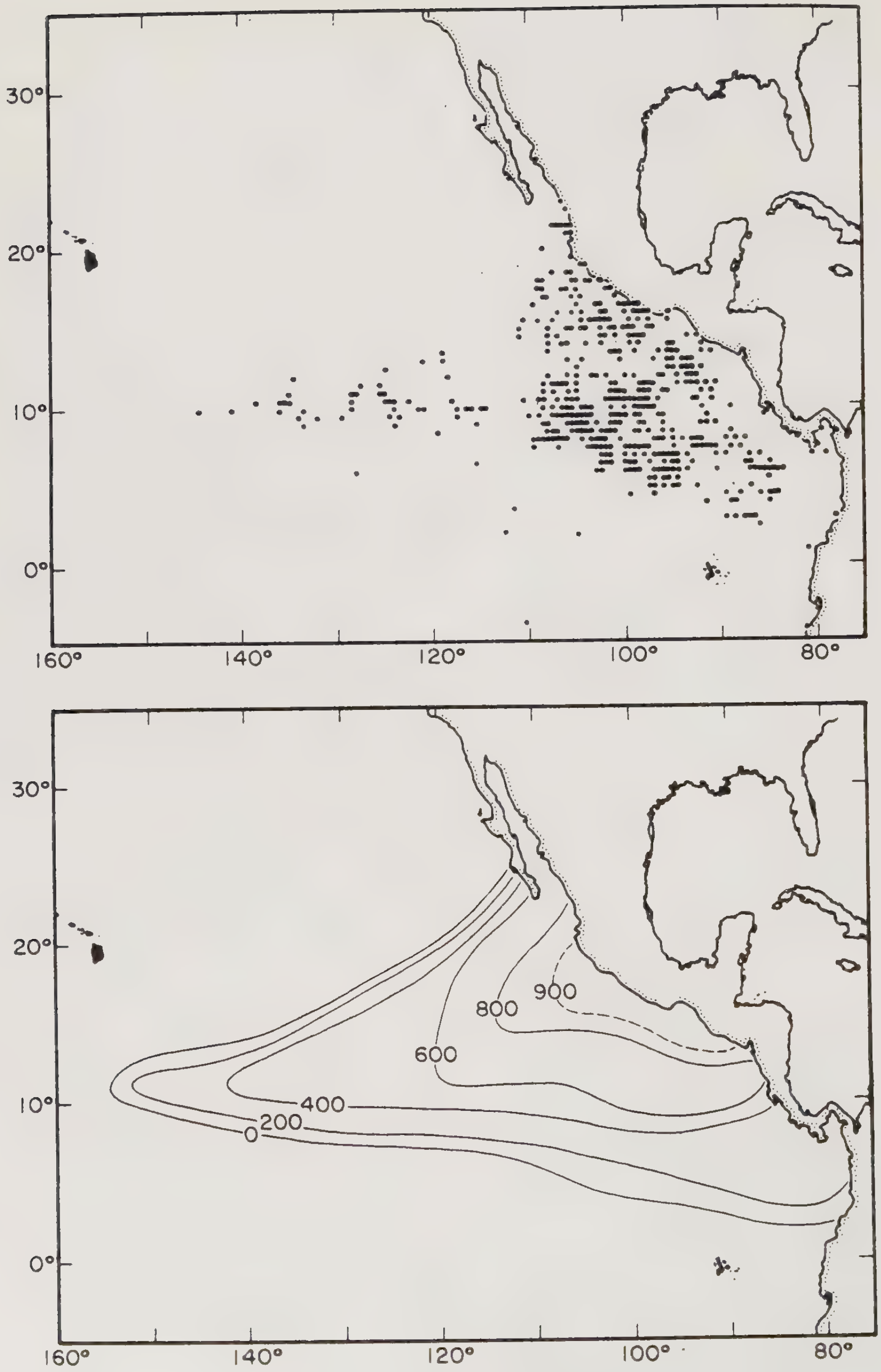
30°
20°
10°
0°
160°
140°
120°
100°
80°
900
800
600
400
200
0

FIGURE 1.—Comparison of the known occurrence of spotted porpoise in the eastern Pacific (above) with average thickness of the subsurface layer of water (contours in meters) in which the dissolved oxygen is less than 0.25 ml/liter (below, after Knauss 1963). The entire layer lies above 1,000 m.

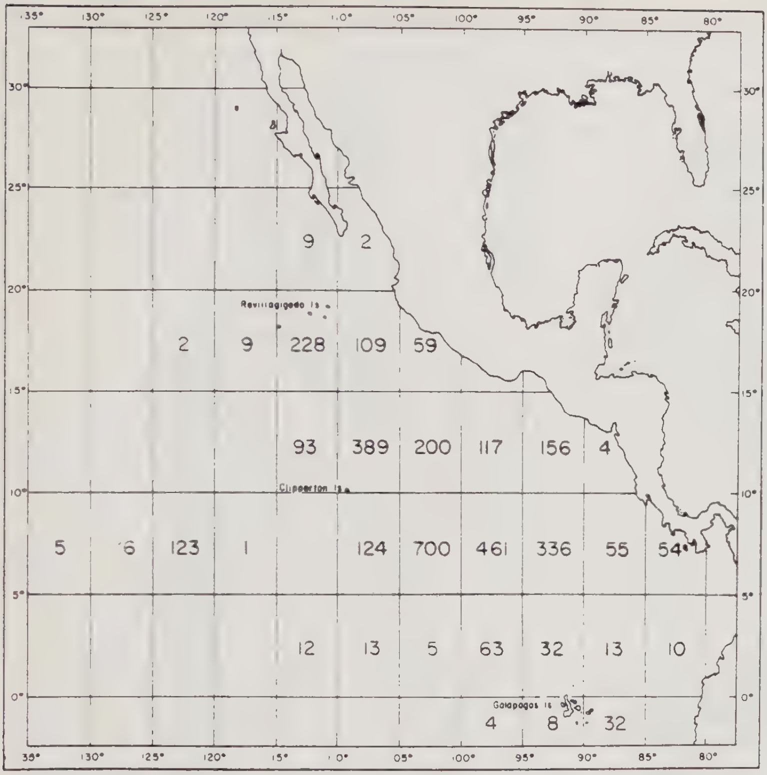

FIGURE 2.—Samples of spotted porpoise used in life history studies by 5° square. Does not include specimens that were not at least measured.

Because the field program is a continuing one, the sample sizes for the various analyses were different and depended on how much material was available at the time each analysis commenced. Restrictions on sample size are set out in the text below.

Laboratory Procedures

Fetuses were measured with dial calipers or with calipers mounted on a 1-m stick. Postnatal animals were weighed to the nearest pound on platform scales. Fetuses were weighed to the nearest gram on a triple beam balance. Testes were weighed to the nearest gram on a platform balance. A 1-cm^3 cube from the center of each testis[5] and a similarly sized sample of the epididymis from midlength of the testis were sectioned and stained with hematoxylin and eosin. The mounted sections were subsequently examined under a compound microscope.

Ovaries were weighed to the nearest 0.1 g on a platform balance. They were then cut into transverse sections approximately 1 mm thick with a scalpel and the sections examined under a dissecting microscope. The corpora albicantia in each ovary were scored to eight categories based on size, color, vascularization, and gross appearance (categories described below). If a corpus luteum was present, it was measured with dial calipers to the nearest millimeter in its three largest dimensions. The diameter of the largest follicle was measured to the nearest 0.1 mm.

Age was estimated for 442 animals by examination of dentinal layers in the teeth. Three or four teeth were extracted from the lower right tooth row at approximately midlength and mounted on wooden blocks in dental wax or plastic resin. A longitudinal section 0.012 inch (0.31 mm) thick was cut from each tooth with a diamond saw. The sections were cleared for several days in a 1:1 mixture of glycerine and 95% ethanol, mounted under cover slips in balsam, and examined with transmitted light under a compound microscope at approximately 30 diameters. One postnatal layer was considered to consist of an opaque subunit and a translucent subunit (Figure 3). The layers in most of the teeth examined were not as well-defined or as regular in thickness as those illustrated by Kasuya (1972) for *Stenella coeruleoalba* or by Klevezal' and Kleinenberg (1969) for *Delphinus delphis*. Teeth from 39 of the 442 animals were completely unscorable, being heavily worn or showing no discrete layers in the sections examined. All the teeth were scored several times, over a period of several months, without referring to specimen numbers or to values obtained previously, until the scorer felt confident of the results. The values used in the analyses are those obtained in the final round of scoring. The teeth were scored to the nearest postnatal layer when possible, or a range, e.g., "8 to 10 layers," was estimated. Average accuracy is estimated at ±1 layer for teeth with 5 layers or less and ±2 layers for teeth with 5 to 12 layers. Convoluted secondary dentine was present in most of the teeth with more than 12 layers, making counts very difficult and of dubious reliability. We feel that the counts for many of these teeth are probably underestimates. Teeth in which the pulp cavity was entirely closed in all sections examined were scored as "occluded."

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[5] Some early samples were taken near the dorsal surface of the testis. Tubule diameter in these was subsequently found not to differ relative to length, weight, and age of the animal from that in those taken at the center of the testis, and the lots were therefore combined for analysis.

The NORMSEP computer program was used to define modes in the length-frequency distributions for fetuses. The program was written by Hasselblad (1966) and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates the mixture of normal length distribution into its components, assuming that the lengths of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained.

GROWTH

Length at Birth

Average length at birth of 82.5 cm was obtained from a linear regression line based on 3-cm groupings of fetuses and neonatals (Figure 4). The largest fetus of the 461 examined was 904 mm long. The smallest neonatal animal was 780 mm long. Eighty-six calves and fetuses between 73 and 94 cm were measured in random samples. Assumptions inherent in the method used to arrive at this estimate are that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. For example, if neonates were less likely to be included in the samples than were pregnant females, average length at birth would be overestimated. Other potential sources of error are differential rates of prenatal and postnatal natural mortality and premature births caused by stresses imposed by pursuit and by capture in the purse seine.

Gestation Period and Fetal Growth

The most commonly used method for estimating the gestation time of cetaceans is that of Huggett and Widdas (1951). They showed that for a variety of mammals of widely different orders, a plot of the cube root of fetal weight on age is linear except during the first part of pregnancy, when growth is exponential. Their model can be expressed in the general formula $W^{1/3} = a(t - t_0)$, where W = weight, t = age, a = the "*Specific Fetal Growth Velocity*," and t_0 = "the intercept where the linear part of the plot, if produced backwards, cuts the time axis." Laws (1959) applied the method of Huggett and Widdas to fetal length/time data for three odontocetes (*Physeter catodon*, *Delphinapterus leucas*, and *Phocoena phocoena*) and obtained estimates of gestation periods (15, 14, and 11 mo, respectively). He assumed that weight is proportional to the cube of length and used the form $L = a(t_g - t_0)$, where L = length. This assumption is not entirely correct (see length-weight results below), but is a close enough approximation of the real relationship between length and weight to allow its use in estimating gestation period. Laws' estimates corresponded closely with other estimates obtained by more direct methods. Laws' version of Huggett and Widdas' method is used here.

A gestation period of 11.5 mo was obtained from an analysis based on 281 fetal and postpartum specimens collected in January, February, March, April, May, and October 1972 (Figure 5). The January-May samples comprised all of the fetuses of all of the females examined. The postpartum samples in these months were not random and are therefore not included. The October samples were random over all age-classes in the catch; therefore, all specimens less than 160 cm long, approximately the length at onset of puberty (Harrison et al. 1972), are included in the plot. Obvious modes are present in the length distributions (seasonal-

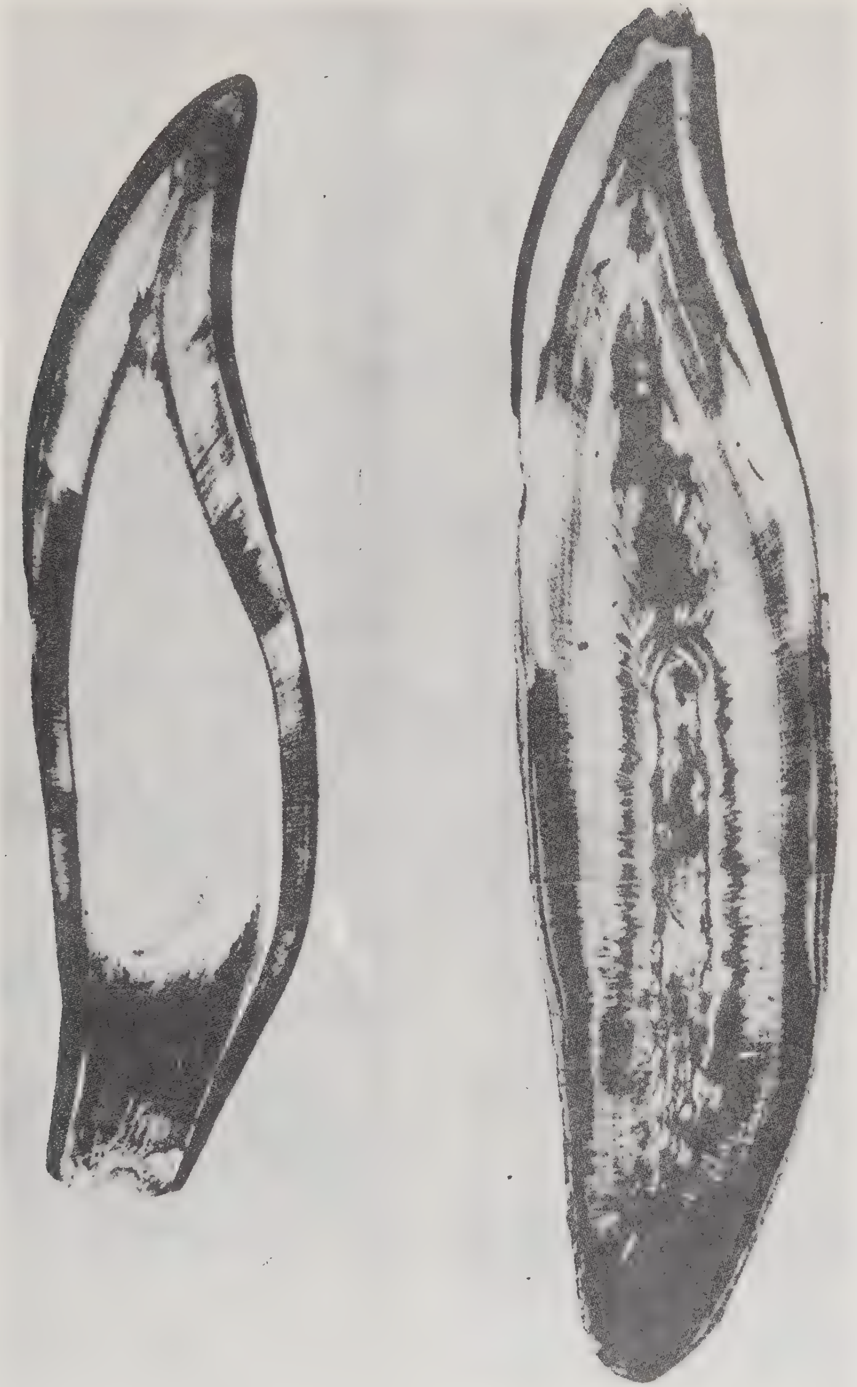

FIGURE 3.—Longitudinal thin sections of teeth from two specimens of *Stenella attenuata* from the offshore eastern tropical Pacific. (Left) field number CV300 male, 144 cm, with two postnatal dentinal layers; (right) number LR55 female, 191 cm, with 13 layers.

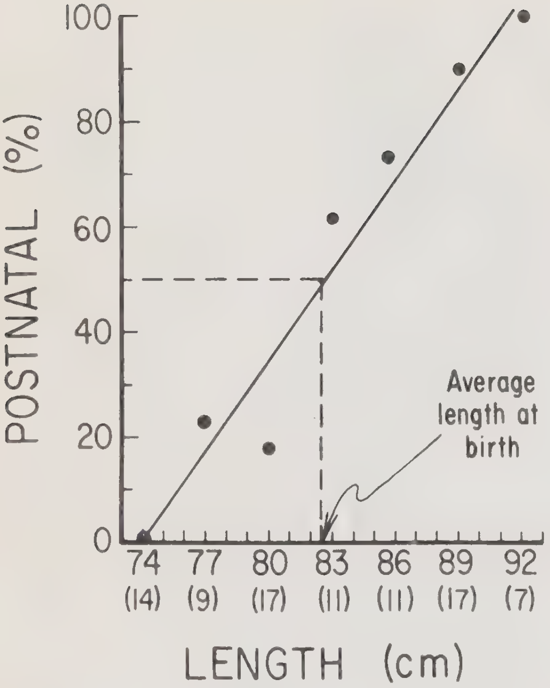

FIGURE 4.—Linear regression analysis of percent postnatality on body length for 86 fetuses and calves of *Stenella attenuata* from the offshore eastern Pacific grouped in 3-cm intervals. Sample size for each 3-cm interval in parentheses.

ity is discussed below). Apparent progression of the smaller mode in the January 1972 sample is consistent with a gestation period of roughly 1 yr. Sample sizes for the other apparent modes are not large enough for similar analysis. Linear regression analysis of the modal lengths plotted on month (Figure 6) yields an estimate of the slope to use in Laws' equation:

$$L = 8.283\ (t - t_0),\ \text{or}$$
$$\text{length at birth} = 8.283\ (t_g - t_0)$$

with $(t_g - t_0)$ (using months of 30.4 days) = 9.96 mo or 303 days, where t_g = total gestation period.

Laws (1959) proposed that t_0 for length data is slightly less than for weight data and assumed $t_{0_{Ln}} = 0.9\ t_{0_{wt}}$. Roughly interpolating between Huggett and Widdas' values for $t_{0_{wt}}/t_g$ of 0.1 for $t_g > 400$ days and 0.2 for $t_g = 100$ to 400 days (using provisional $t_g \cong 330$ days to enter the iteration) (Figure 7) and applying Laws' correction, $t_{0_{Ln}}$ of $\cong 0.135\ t_g$ is obtained. This value yields an estimate of gestation time of 11.5 mo (349 days). The estimate of t_0 (47 days) is crude, but the true value probably lies between $0.12\ t_g$ and $0.15\ t_g$. We therefore estimate the gestation period to be 11.5 ± 0.2 mo (interval between estimates using $t_0 = 0.12\ t_g$ and $0.15\ t_g$), or 11.3 to 11.7 mo.

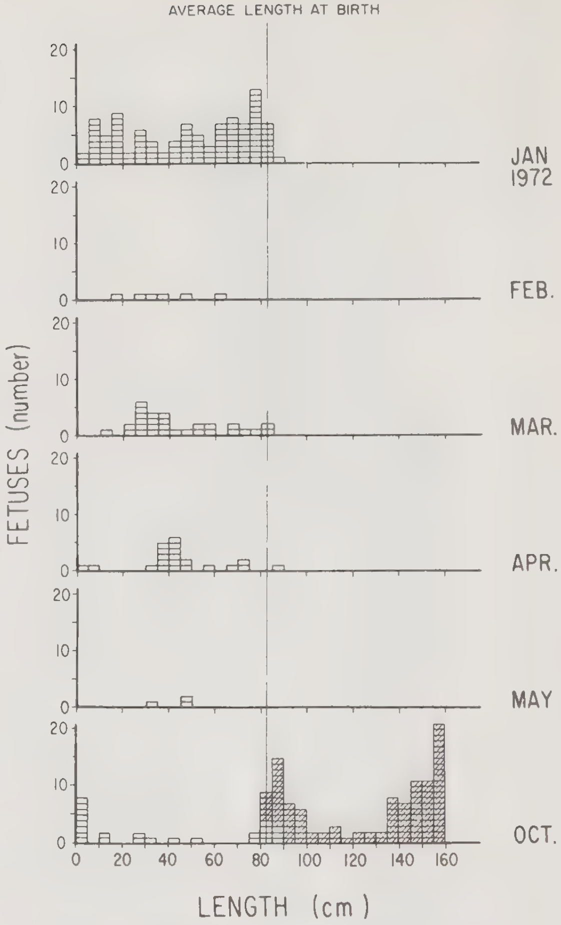

FIGURE 5.—Length-frequency distributions by month for 281 fetal (open) and young (hatched) postnatal specimens of *Stenella attenuata* captured by tuna seiners in the offshore eastern tropical Pacific in 1972.

Postnatal Growth

The same cohort used for analysis of fetal growth can be followed through the samples until approximate length of 125 cm (Figure 8) at the age of approximately 8.5 mo. In order to optimize resolution, 4-cm intervals were used, and the samples for April, May, and June were combined. Modes were estimated with NORMSEP.

A linear regression line through the modal lengths yields the postnatal growth equation

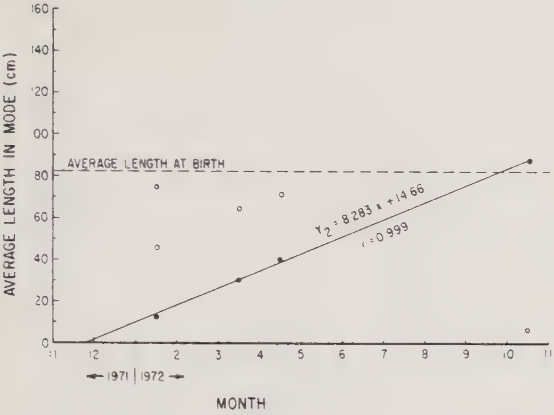

FIGURE 6.—Linear regression analysis of modal lengths of fetal and neonatal specimens of *Stenella attenuata* (from Figure 4). Open circles are modes not included in the analysis. Modal lengths defined with computer program NORMSEP (see Materials and Methods).

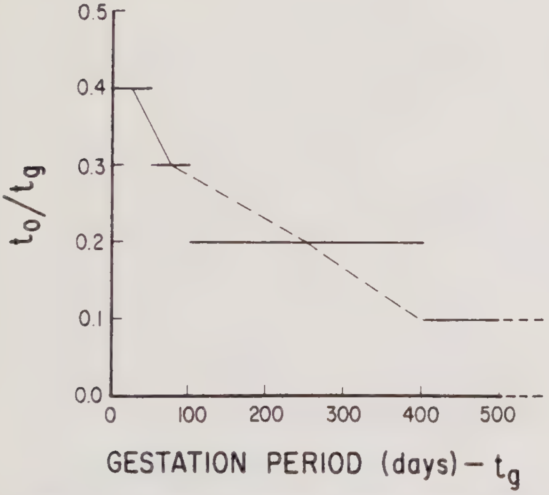

FIGURE 7.—Ratio t_0/t_g interpolated between empirical estimates of Huggett and Widdas (1951)—". . .for gestation times up to 50 days $t_0 \triangleq 0.4 \times$ (gestation time), from 50-100 days $t_0 \triangleq 0.3 \times$ (gestation time), from 100-400 days $t_0 \triangleq 0.2 \times$ (gestation time), over 400 days $t_0 \triangleq 0.1 \times$ (gestation time)."

$$L = 82.5 + 5.42\,t,$$

where L = length in centimeters
t = postnatal age in months.

Analysis Based on Analogy with Other Cetaceans

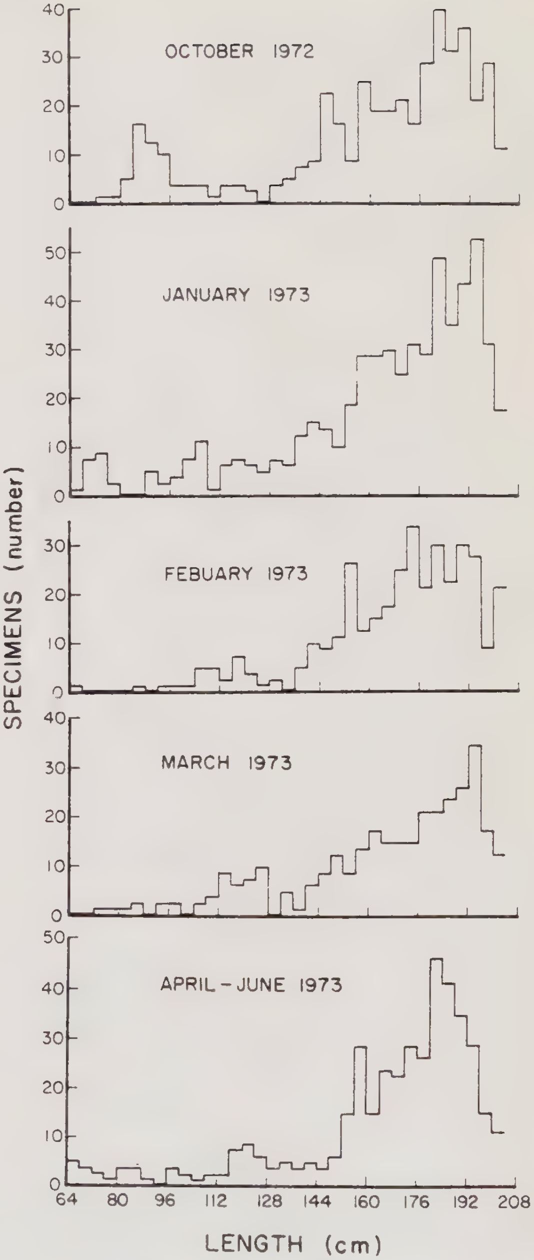

FIGURE 8.—Length frequencies of fetuses and postnatal specimens of *Stenella attenuata* between 64 and 204 cm long, of both sexes, by month.

Fetal growth in length of cetaceans, except for an initial slow phase (t_0), is nearly linear. Postnatal growth during at least a period equivalent in length to the gestation period is also nearly linear, but at a lower rate. The difference between the

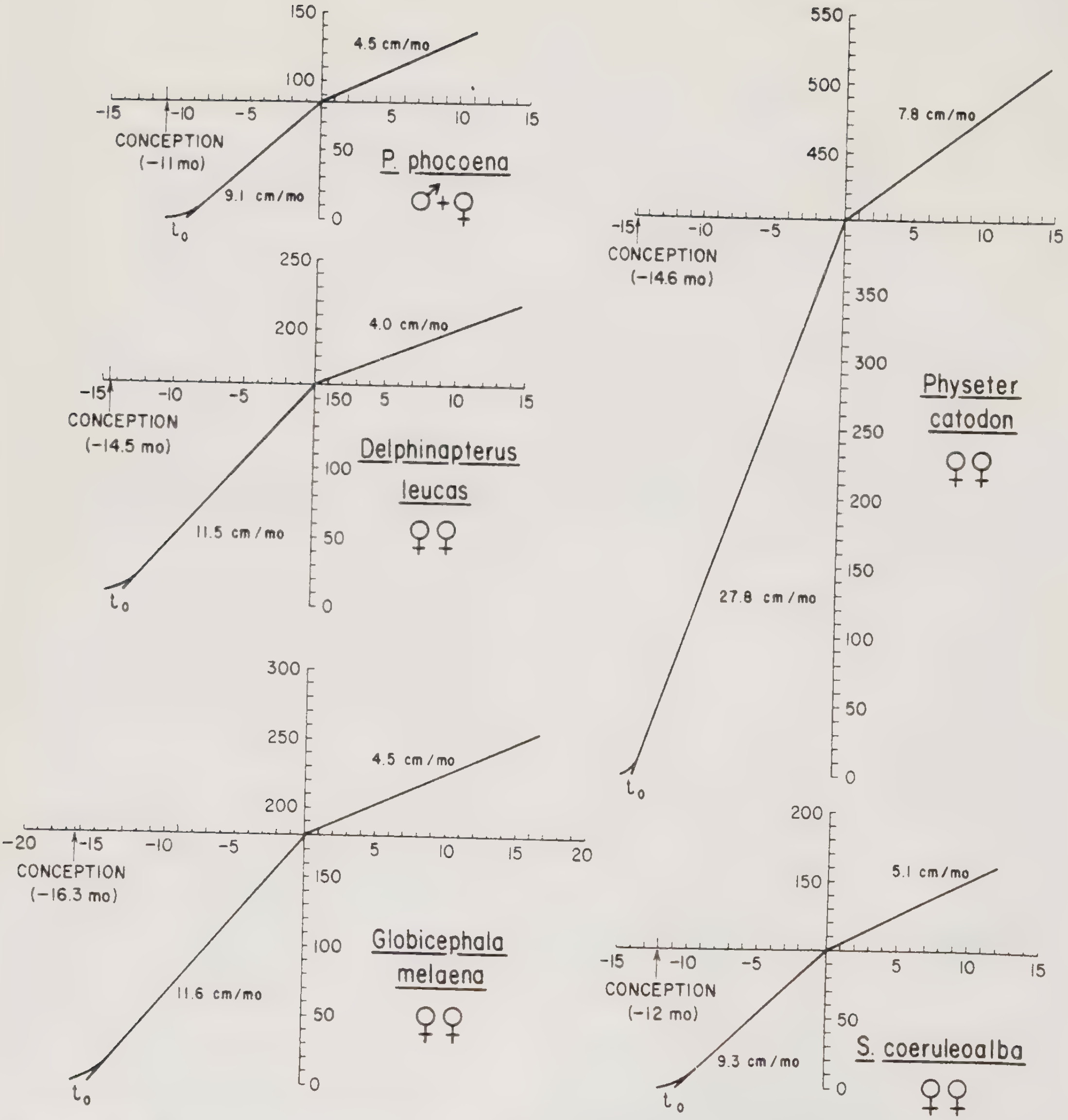

FIGURE 9.—Fetal growth and average postnatal growth during a period equal to the gestation period in five odontocete cetaceans: *Phocoena phocoena* (gestation period and postnatal growth from Møhl-Hansen 1954; t_0 from Laws 1959; length at birth from Fisher and Harrison 1970); *Delphinapterus leucas* (from Brodie 1971); *Globicephala melaena* (from Sergeant 1962); *Physeter catodon* (from Best 1968, 1970); and *Stenella coeruleoalba* (from Kasuya 1972).

fetal rate and the average rate during a postnatal period equal to the gestation period differs among the five odontocete species for which sufficient data exist (Figure 9) and is correlated with length at birth (Figure 10). The least-squares line for log of the difference between fetal and postnatal growth rates (Y) on log of length at birth (X) yields $Y = -1.33 + 0.997X$, from which a predicted Y of 3.75 cm/mo is estimated for *S. attenuata* and an average growth rate in the first year of 4.66 cm/mo is estimated. This average rate is close to those for the other three delphinids (5.1 for *S. coeruleoalba*,

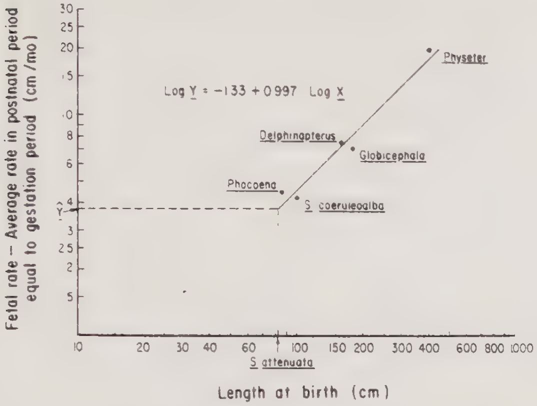

FIGURE 10.—Relationship of difference between fetal growth rate during linear phase and average growth rate during postnatal period equal to gestation period to length at birth in five odontocete cetaceans. Line is linear regression line of log difference on log length. Data from Figure 11. $\hat{Y}$ is predicted difference for *Stenella attenuata* from the offshore eastern tropical Pacific.

4.5 for *Globicephala*, and 4.5 for *P. phocoena*)[6]; and yields a predicted length at 1 yr of 138 cm.

Length Relative to Tooth Layers

Total length was plotted on number of postnatal layers for 115 males and 306 females (Figure 11). The teeth of five males and three females had completely filled pulp cavities. These are included in the plots in a separate category "occluded."

The plots of means for 2-layer intervals (the points in Figure 12; the curves were fitted as explained below) very closely resemble the growth curve obtained by Sergeant (1962) for *Globicephala*. Asymptotic length (L_∞) for females is approximately 190 cm and for males approximately 200 cm. There appears to be a secondary surge in growth at about 6 layers. With the restriction that the curves must pass through birth length of 82.5 cm and asymptotic lengths of 190 and 200 cm, it is not possible to fit any continuous equation to the data satisfactorily. Continuous curves that fit well at the upper and lower ranges of layer count seriously underestimate length at 5 to 7 layers. Kasuya (1972) also encountered difficulty in attempting to fit a continuous model to growth of a delphinid, *S. coeruleoalba*. Good fits can be obtained, however, by assuming a dynamic growth function. A two-phase version of Laird's (1969) growth model was fitted to the 2-cm means for all males and females, using an iterative least-squares method. The occluded specimens were assigned to the 16+ interval.

Laird's model is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\},$$

where

$L(t)$ = length at time t
L_0 = length at birth (82.5 cm in this case)
t = time (layers in this case)
a = specific rate of exponential growth
α = rate of decay of exponential growth.

This model assumes that an organism's growth pattern is determined at conception. The fitted parameters a and α express the premise that "growth is fundamentally exponential (implied by the normal binary fission of cells), and it also undergoes exponential retardation by some as yet unknown physiological mechanism" (Laird 1969).

In the two-phase approach, separate equations were simultaneously fitted to the upper and lower range of means. The assumptions were made that juvenile growth is the same for males and females (supported by the data) and that the growth discontinuity comes at about the same age for males and females. The only fixed point was 82.5 cm at 0 layers (birth). The convergence point (inflection in the growth curve) was allowed to float to the position that gave the best fit, with males and females considered jointly for lesser ages. The equations converged at 5.59 layers (rounded off to 6 below) at which predicted length is 159.9 cm. The fit is excellent for females (Figures 11, 12). Asymptotic length is 190 cm at predicted age of 18 layers. Average length of adult females (those with ovarian scars) is 187.3 cm, based on a sample of 555 (Perrin 1975). The largest female of 2,138 measured was 220 cm long. The equation for juvenile growth to less than 6 layers is

$$L = 82.5 \exp\left\{\frac{0.4817}{0.7172}\left[1 - \exp(-0.7172t)\right]\right\},$$

where L = length, in centimeters
t = age in layers.

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[6] Fisher and Harrison (1970) stated that their data suggest that *Phocoena* in Canadian waters grows approximately 30 cm during the first year of life, or at an average rate of about 2.5 cm/mo, as opposed to the 4.5 cm/mo hypothesized by Møhl-Hansen (1954). However, they also suggested, and their figure 2 showed, an average rate of at least 5 cm/mo during the first 4 mo. It seems unlikely that the rate would drop to an average of ~ 1.25 cm/mo in the remaining 8 mo of the first year.

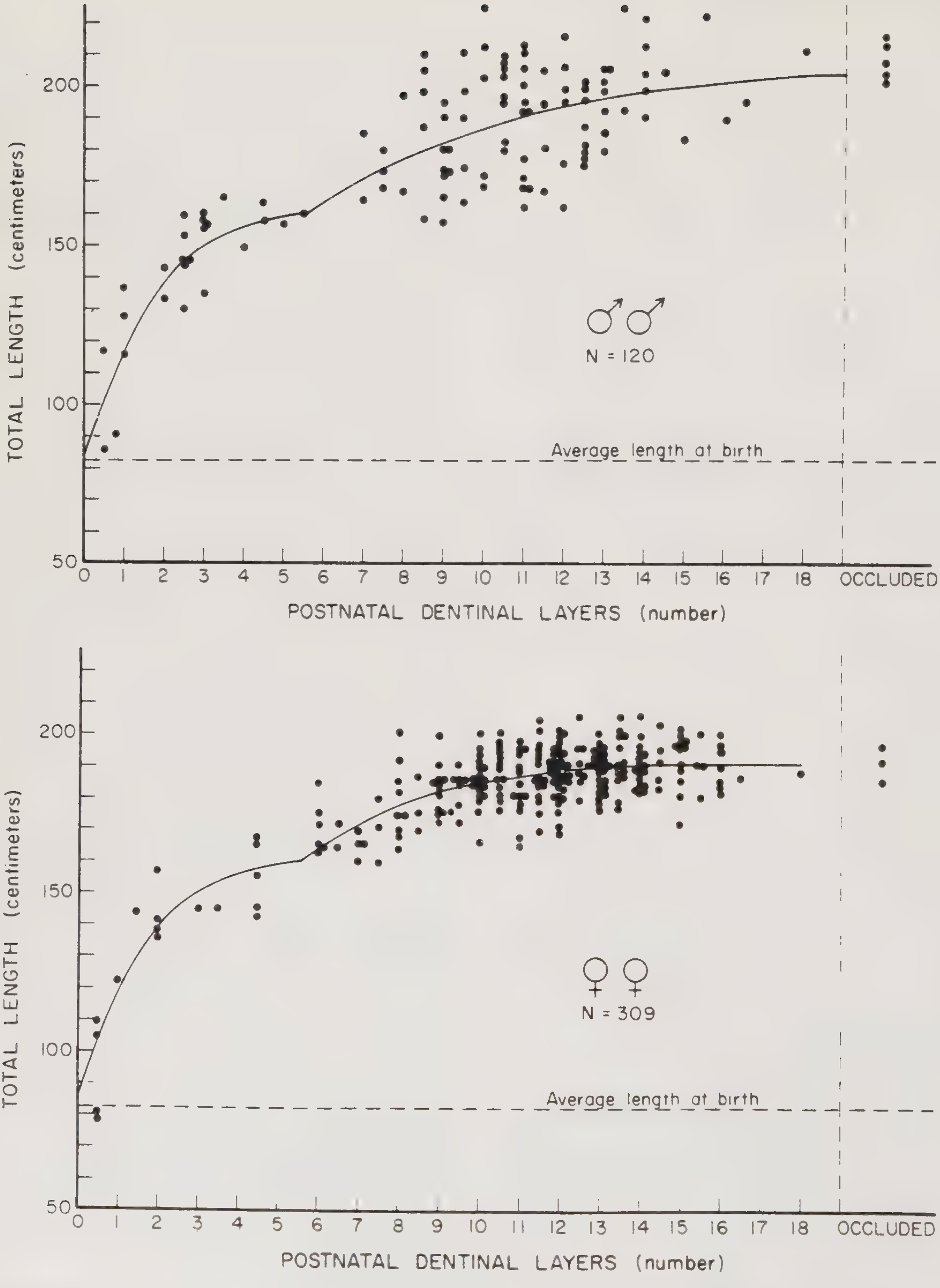

FIGURE 11.—Scatterplots of body length on number of postnatal dentinal layers from males (top) and females (bottom) of *Stenella attenuata* from the offshore eastern Pacific. Lines are fit to the growth model (see text).

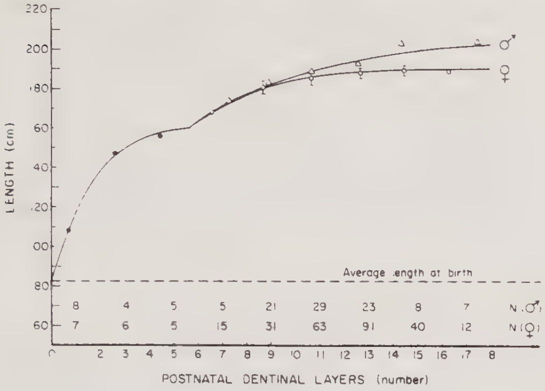

FIGURE 12.—Fit of the double Laird growth model (see text) to 2-cm mean values of body length on number of postnatal dentinal layers for males and females of *Stenella attenuata* from the offshore eastern Pacific. For samples greater than 30, ± standard errors indicated as vertical line.

For females with 6 or more layers, the growth equation is

$$L = 159 \exp \left\{ \frac{0.0657}{0.3707} \left[1 - \exp\left(-0.3707(t - 5.588)\right) \right] \right\}.$$

In this case, both the growth rate and the rate of decay of growth are sharply lower than for juveniles.

The fit for males is not as good (Figures 11, 12) as it is for females, probably due to greater variability and to inadequate sample sizes for the two oldest strata (the tooth-reading effort was concentrated on females because of their importance in population dynamics). Another possible explanation for the relatively poorer fit for males is that growth (real, or as inferred from tooth layers) in adult males is more complex than in adult females, and a model more complex than the Laird model is called for. Inferred asymptotic length is 206 cm, achieved at predicted age of 26 layers. Average length of adult males (defined as those having testes weighing 200 g or more) is 200.7 cm, based on a sample of 253 (Perrin 1975). The largest male of 1,083 measured was 226 cm long. The growth equation for males with 6 or more layers is

$$L = 159.5 \exp \left\{ \frac{0.0524}{0.2032} \left[1 - \exp\left(-0.2032(t - 5.588)\right) \right] \right\}.$$

The secondary growth rate (a, 0.0524) is very slightly smaller than for females, but the rate of decay (α, 0.2032) is sharply smaller, reflecting the attainment of greater size in males. The equations rearranged and reduced for estimating age (in terms of layers) from length are

$$t(\text{M and F} < 160 \text{ cm}) = -1.394 \ln (7.531 - 1.48 \ln L)$$

$$t(\text{F} \geq 160 \text{ cm}) = 5.588 - 2.698 \ln (29.606 - 5.64 \ln L)$$

$$t(\text{M} \geq 160 \text{ cm}) = 5.588 - 4.921 \ln (20.669 - 3.878 \ln L).$$

Note: These equations should not be used to estimate age from length except for grouped samples of smaller animals (about 180 cm or less), for which growth rate is still large compared to individual variation in length.

The juvenile growth curve based on tooth layers can be calibrated for the first year by comparison with the growth curve derived from analysis of modal progression (above) and by deduction from what is known about juvenile growth of other odontocetes (the fetal-postnatal growth argument above). Estimated average length at 8 mo based on analysis of modal progression is 125.5 cm. The predicted number of layers at that length (Figure 12) is 1.53. If the average growth rate during the first year is assumed to be the same as the average during the first 8 mo, the predicted number of layers at 1 yr ($1.53 \cdot 12 \div 8$) is 2.3. This extrapolation, however, is a slight overestimate, because while growth during the first year in delphinids is approximately linear, there is some decay of rate. The predicted number of tooth layers (using Figure 12) at 138 cm, the above-predicted length at 1 yr based on camparison with other odontocetes, is 2.0. It seems safe to assume that about 2 layers are laid down during the first year of life.

Calibration of the remainder of the tooth-layer curve is more difficult. Kasuya et al. (1974) examined the innermost layer in teeth of *S. attenuata* and related type and thickness of layer to season of capture. They concluded that one layer (one transparent plus one opaque subunit) represents 1 yr of growth. We found no correlation between thickness of the innermost layer and season of capture. Almost all of the samples for which teeth were sectioned, however, were collected in the first few months of the year. Lacking such direct calibration, several alternative possibilities can be examined. The results, however, must remain tentative and inconclusive until growth has been monitored directly in one or more captive or free-ranging, tagged individuals.

Some alternatives that can be considered are:

1. Two layers per year until the teeth are occluded.
2. Two layers in the first year and one per year thereafter until the teeth are occluded.
3. Two layers per year until puberty (about nine layers in males and seven in females; see section below on age at puberty), and one per year thereafter.

This list of alternatives can be extended to great length by making assumptions such as that layers are laid down at irregular intervals, males and females lay down layers at different rates, layers disappear with age, etc., but the above are probably the main possibilities that should be considered. All references below to age are in terms of layers, with the above alternative possibilities considered or implied. None of the alternatives can be eliminated with certainty. One tooth layer deposited per year has been inferred for the western Pacific population of *S. attenuata* by Kasuya et al. (1974). One layer per year has also been suggested for other closely related delphinids, including *S. coeruleoalba* (Kasuya 1972) and *Tursiops truncatus* (Sergeant et al. 1973). Two tooth layers per year have been found in *Delphinapterus leucas* (Sergeant 1973), but this form is less closely related to *Stenella*. Thus, there is more support in the literature for the one-layer-per-year model (number 2 above) than for the others.

Length-Weight Relationships

Length-weight relationships were determined for 218 fetuses, 66 postnatal males, and 33 nonpregnant, postnatal females by using linear regressions of log weight on log length.

Fetuses

The fetuses ranged from 20 to 897 mm long and weighed from 2 to 7,588 g. Ten fetuses less than 20 mm long were not included. The regression equation is

$$\log W = 3.5532 + 2.501 \log L,$$

where W = weight in grams
L = length in millimeters.

In exponential form, the relationship is

$$W = 2.79 \times 10^{-4}\ L^{2.501}.$$

Females

The females ranged from 100 to 200 cm and weighed from 12.0 to 69.1 kg. The regression equation is

$$\log W = -4.1576 + 2.6120 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 6.95 \times 10^{-4}\ L^{2.612}$.

Males

The males ranged from 86 to 218 cm and weighed from 6.8 to 90.0 kg. The regression equation is

$$\log W = -4.7135 + 2.873 \log L,$$

where W = weight in kilograms
L = length in centimeters, or in exponential form, $W = 1.93 \times 10^{-5}\ L^{2.873}$.

The slopes of the regression equations are statistically different (t-test at $\alpha = 0.05$) for males and females. Males are lighter for their length at birth, and heavier for their length after about 135 cm has been attained.

Color Pattern

Perrin (1970b) has previously described the development of the color pattern of *S. attenuata* in the offshore eastern Pacific. The animal begins life unspotted, develops dark spots ventrally that later coalesce, as light spots develop dorsally. The ontogenetic continuum can be divided into five stages as defined below and as shown in Figures 13 and 14:

1. *Newborn stage.* Dark purplish-gray dorsal surfaces and lateral blazes, with white ventral surfaces and no spots; about 80 to 160 cm.
2. *Two-tone stage.* General two-tone pattern with dark-gray surfaces above, lighter gray lower surfaces, and a well-defined pattern in varying shades of gray about the head and flippers; no spots; about 95 to 175 cm.

The division between this and the previous category is somewhat subjective and arbitrary.

3. *Speckled stage.* Same as two-tone but with discrete, very dark-gray spots on the ventral surfaces; discrete light-gray spots on the upper, darker surfaces present on some animals but lacking on others; about 140 to 190 cm.

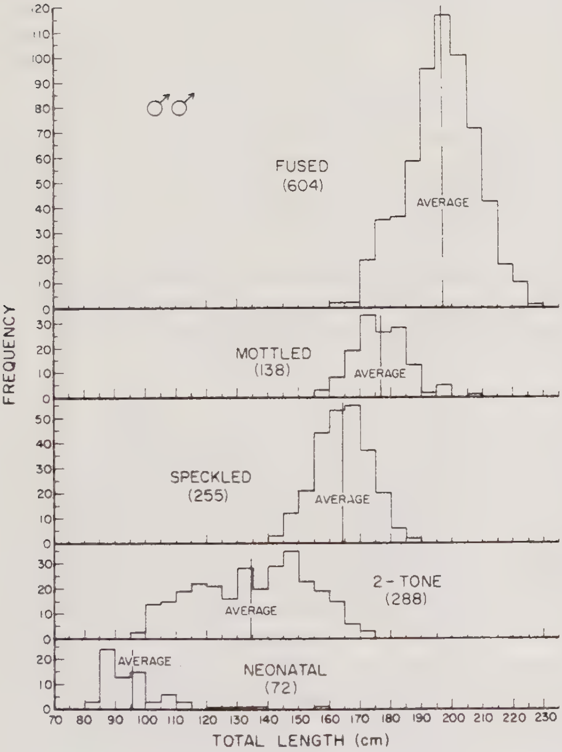

FIGURE 13.—Length-frequency distributions of males of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phase.

4. *Mottled stage.* Ventral spots converging and overlapping in places, but patches of the lighter gray background still visible, yielding a mottled effect; discrete or merging light-gray spots present on the upper surfaces; about 155 to 210 cm.
5. *Fused stage.* Ventral spots completely convergent, to give the effect of a uniform, medium-gray to dark-gray surface; on close inspection, the individual overlapping spots still discernible; about 160 to 230 cm.

REPRODUCTION

Seasonality

Nishiwaki et al. (1965) suggested that *S. attenuata* in Japanese waters breeds in the spring and in the autumn. Harrison et al. (1972) stated that lengths of fetuses indicate that parturition in the eastern tropical Pacific (of *S. graffmani* = *S. attenuata*) also occurs both in the autumn and in the spring. The postnatal length-frequency data for large samples (Figures 15, 16; April 1968 and October 1972, for example) support the thesis of major reproductive seasons in spring and autumn but also suggest that there is a reproductive peak in summer as well. There is year-to-year variation in the timing of reproductive peaks, and there is some reproduction occurring throughout most of the year. It is difficult to define the reproductive seasons with precision because most of the sampling effort was in the early (January-April) and late (October-December) parts of the calendar year. The sampling intersected obvious calving seasons in April 1968, January 1972, October 1972, January 1973, and June 1973 (Figures 15, 16). Calving peaks were probably also present in some of the other sampling months, but the samples were too small to detect them or were biased in some fashion. A summary of predicted birth dates for 373 fetuses more than 15 cm long collected in 1971, 1972, and 1973, however, indicates that there may have been three calving peaks in each of the 3 yr (Figure 17). In each year there was a definite calving low in winter. The synchrony was diffuse, and some peaks were much sharper than others. The statistical evidence for three annual peaks in calving is weak, and when the data for all years are combined, all that can be said with certainty is that the calving season is prolonged, with a low point in winter and a tendency for high points in spring and fall.

The Male

Sexual development of the male was examined under three criteria: 1) weight of testes, 2) average diameter of seminiferous tubules, and 3) amount of sperm in the epididymis. Each of these was examined relative to total length, weight, and age (number of postnatal dentinal layers).

Weight of the testes (Figure 18) increases precipitously at body length of about 175 to 190 cm,

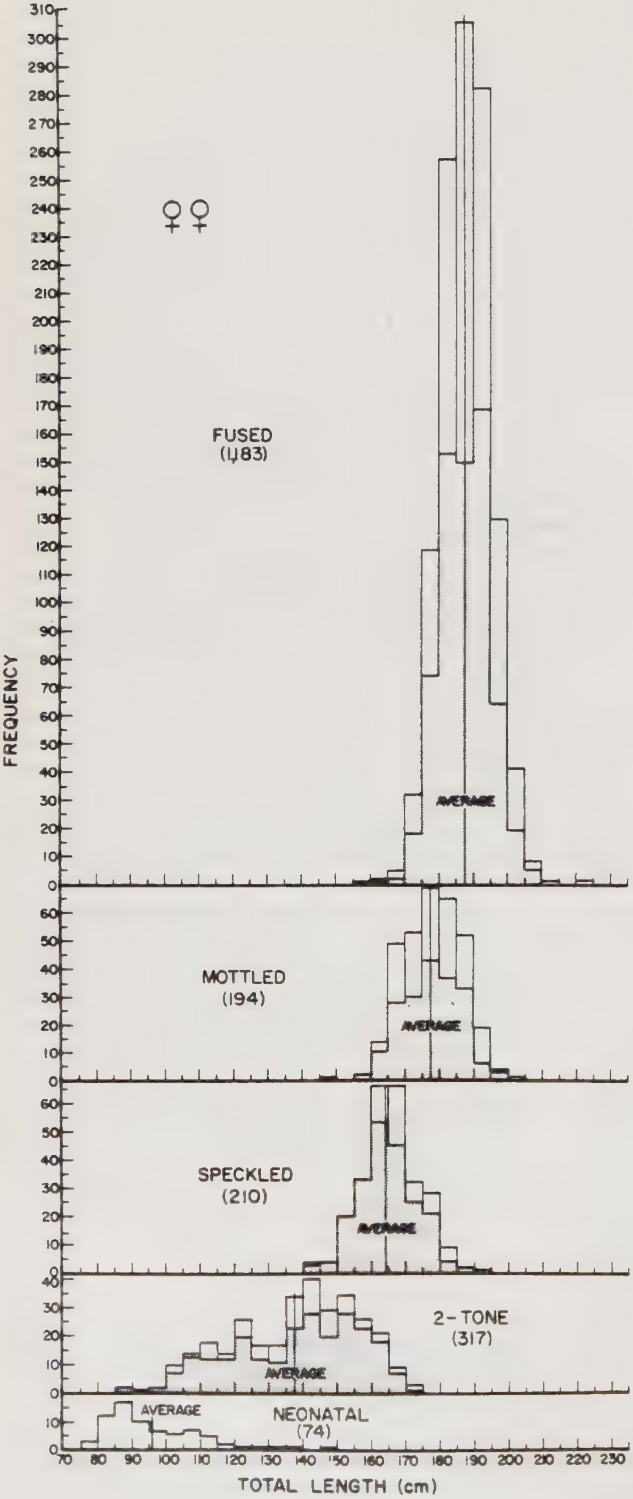

FIGURE 14.—Length-frequency distributions of females of *Stenella attenuata* from the offshore eastern Pacific, by color pattern phases. On cruises between January 1971 and October 1972, adult females (≥160 cm) were selected for measuring and dissection. Earlier and later samples were nonselective. Average lengths for neonatal, two-tone, and fused are based on all the samples (no length bias), and averages for speckled and mottled are based on the nonselective samples (shaded). The analyses of coloration transition are based on all the samples for neonatal-to-two-tone and on the nonselective samples for the remaining three transitions. Size of sample used for calculation of average is given in parentheses.

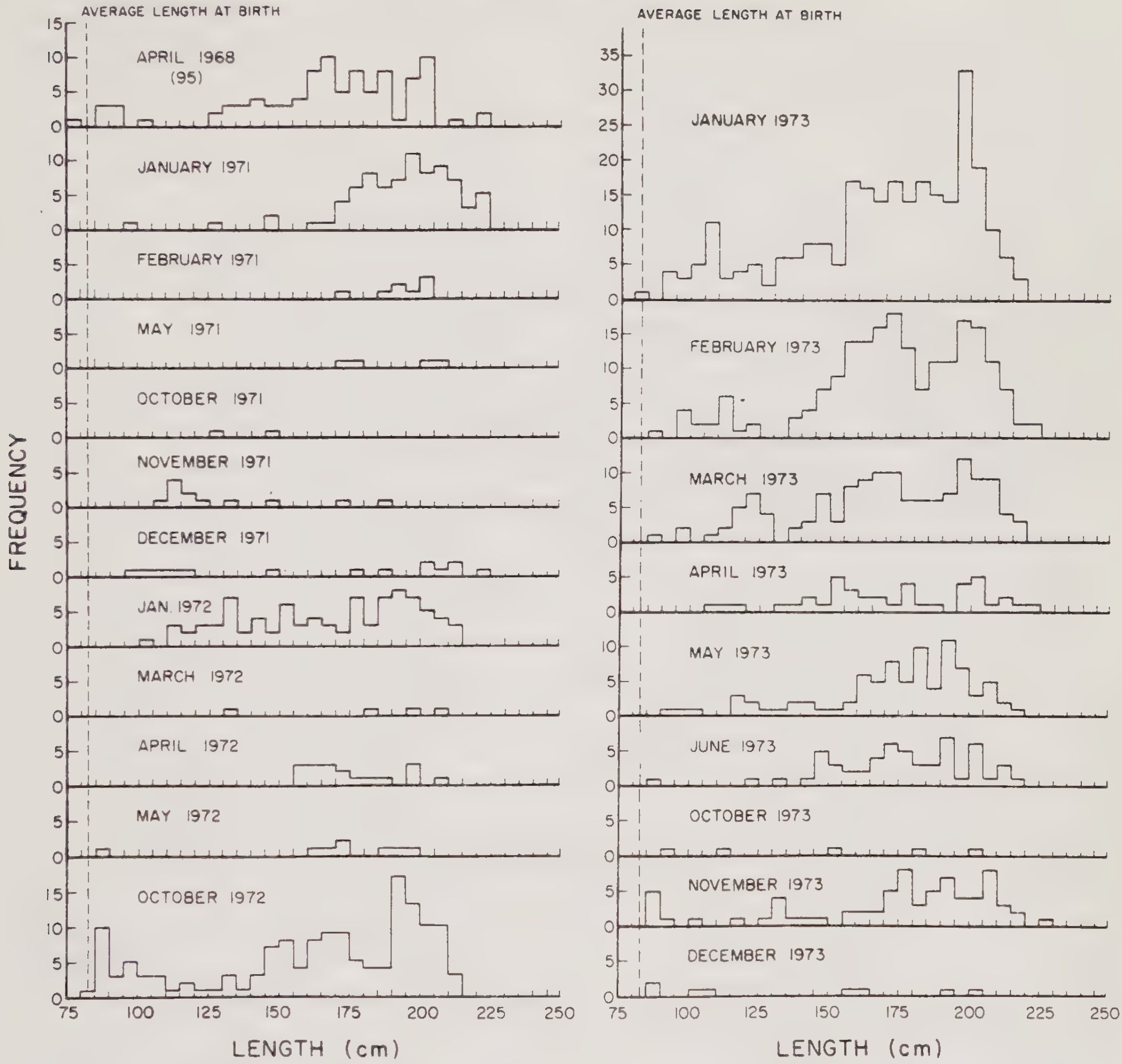

FIGURE 15.—Length-frequency distributions of postnatal male specimens of *Stenella attenuata*, 1968-73, by month.

but in animals larger than about 200 cm, there is little correlation with length. The largest testes encountered weighed 2,400 g and were possessed by a male 196 cm long. However, some males more than 210 cm long had testes weighing less than 300 g. Testes weight begins to increase sharply at 50- to 55-kg body weight and is strongly correlated with weight in larger animals. Males in the sample that weighed more than 70 kg (eight animals) had testes weighing more than a kilogram. The male with the third heaviest testes (2,017 g—heaviest testes for which body weight also available) weighed 80 kg; the heaviest male in the sample weighed 91 kg and had testes weighing 1,348 g. A rapid increase in testes weight (Figure 19) occurs at age 7 to 13 layers, with maximum size increasing until 12 to 16 layers. All animals with more than 14 layers had testes weighing 500 g or more. Again, there is wide variation in testes size relative to age. Part of the variation is ascribable to the considerable error in the estimate of number of dentinal layers (±2 layers for animals with more than 5 to 12 layers, more for older), but it must be concluded that there is probably about a 5-layer period during which the onset of puberty may

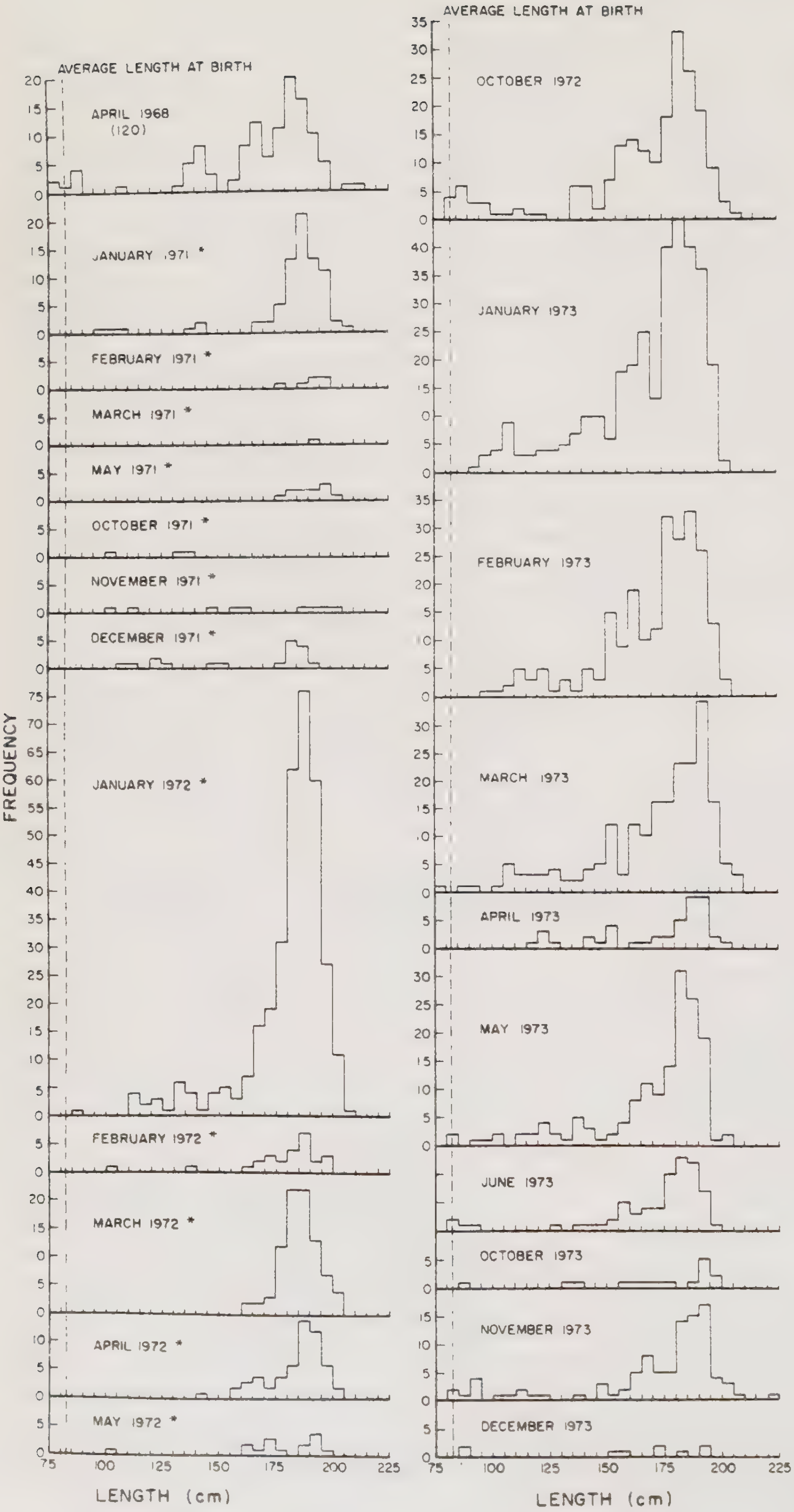

FIGURE 16.—Length-frequency distributions of postnatal female specimens of *Stenella attenuata*, 1968-73, by month.

take place (age about 7 to 12 layers) and that about 2 to 4 layers are required to attain "adult" testes size (500 to 2,000 g). The third largest testes were possessed by an animal (202 cm long, 80 kg, discussed above) that had nonreadable teeth that were worn to the gum in all four tooth rows. Such tooth wear may be a correlate of relatively great age.

The diameter of the seminiferous tubules begins to increase rapidly at body length of about 155 to 170 cm (Figure 20), or at lengths about 15 cm shorter than those at which testes weight begins to increase. Tubule diameter is definitely correlated with body length until at least about 200 cm. The heaviest male (91 kg) had the largest tubules. The plot of tubule diameter on layers (Figure 21) indicates that the tubules enter a rapid development stage at 6 to 11 layers, before the onset of a rapid increase in testes weight (Figure 19). Asymptotic diameter is about 170μm and appears to be attained by 10 to 14 layers.

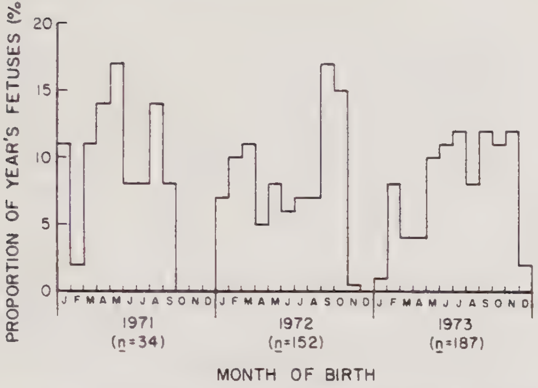

FIGURE 17.—Predicted month of birth for 373 fetuses of *Stenella attenuata*, based on fetal growth curve.

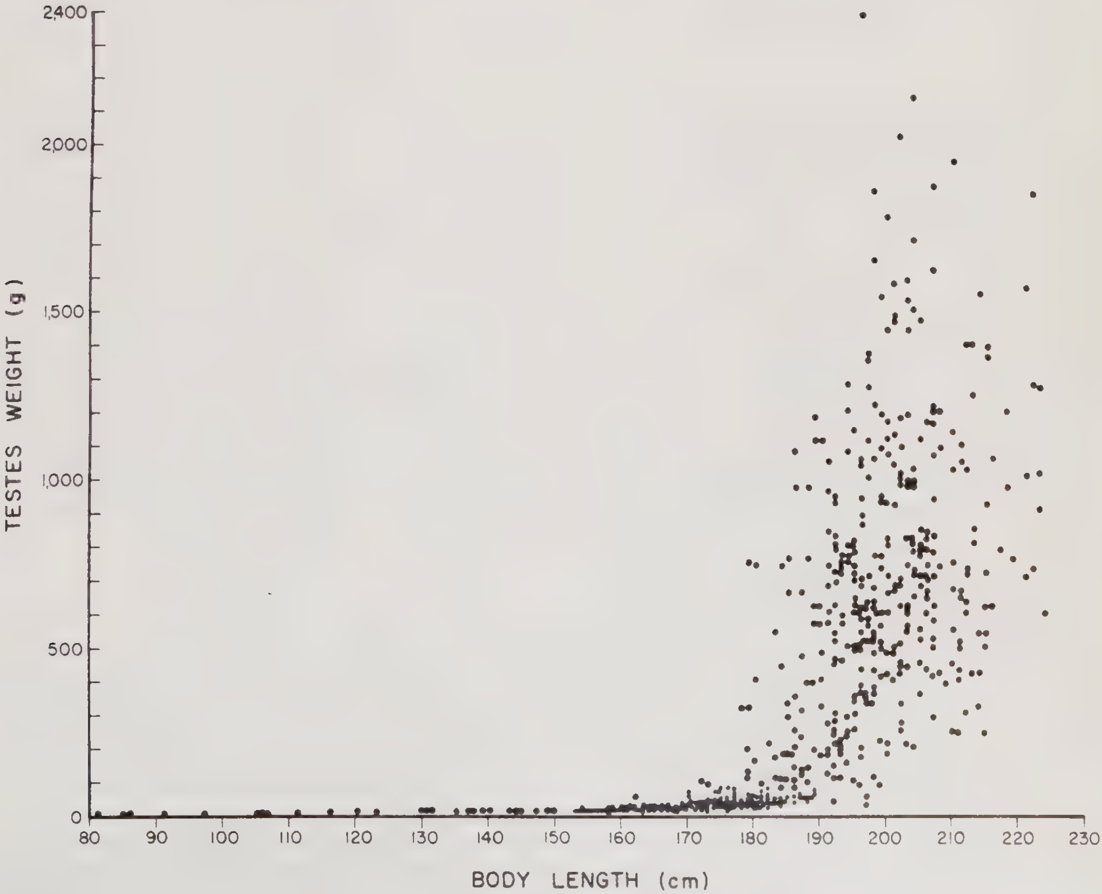

FIGURE 18.—Scatterplot of testes weight on body length in *Stenella attenuata*.

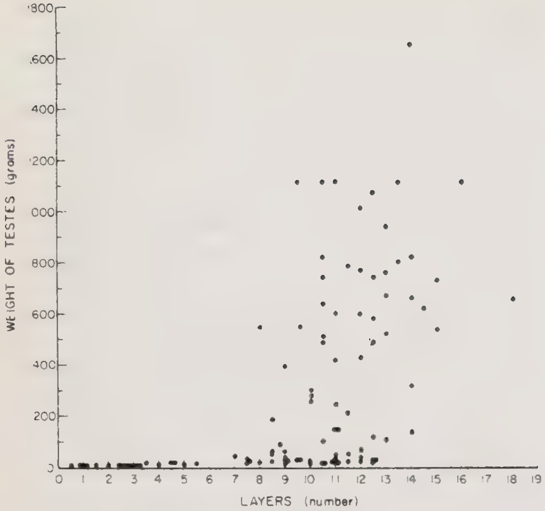

FIGURE 19.—Scatterplot of testes weight on number of postnatal dentinal layers in *Stenella attenuata*.

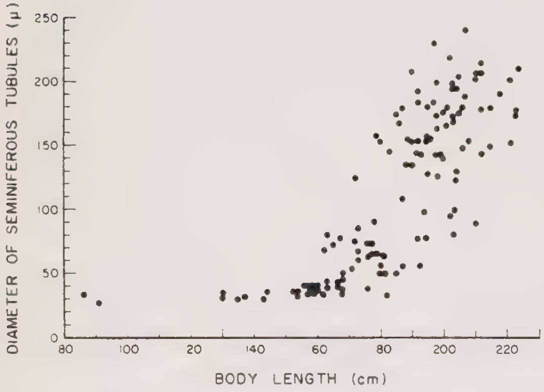

FIGURE 20.—Scatterplot of average diameter of seminiferous tubules on body length in *Stenella attenuata*.

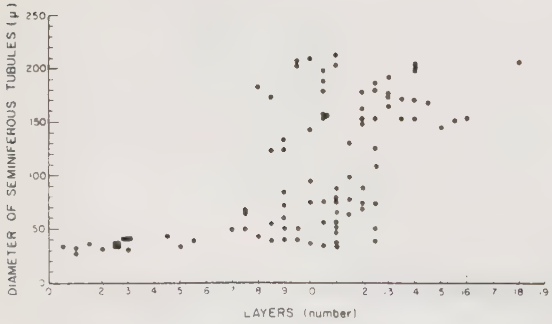

FIGURE 21.—Scatterplot of average diameter of seminiferous tubules on number of postnatal dentinal layers in *Stenella attenuata*.

Sperm in the epididymis were scored as "absent," "present in small numbers," or "copious" (easily seen in the histological sample without searching). The shortest individual with large numbers of sperm in the epididymis was 179 cm long. This animal weighed 62 kg. In animals larger than 180 cm and heavier than 58 kg, presence or absence of sperm in the epididymis bears little relationship to total length. Thirty-six large adults (>200 cm) were equally distributed among the three categories of no sperm, some sperm, and copious sperm.

The smallest testes bearing epididymis with sperm weighed 200 g, and the smallest testes with copious sperm weighed about twice as much. Some animals with testes heavier than 1.5 kg, however, had no sperm in the epididymis. The same pattern of wide variation is apparent in the relationship between epididymis code and layers. The youngest male with sperm in the epididymis had 9 layers. The youngest animal with copious sperm had 10 layers. After about 10 layers, there appears to be no relationship between age and presence or absence of large numbers of sperm.

In summary, the onset of puberty, as indicated by a rapid increase in diameter of seminiferous tubules and increase in testes weight, is at 7 to 12 layers (average ~9 layers; an estimate of ages at puberty) and at lengths of 155 to 170 cm and weights of 40 to 50 kg. Sexual maturity is attained about 2 to 4 layers later, at 10 to 14 layers, ≥180 cm, and ≥58 kg. The midpoint of the range of 10 to 14 layers, or 12 layers, may be taken as an approximation of average age at attainment of sexual maturity. Whether or not males at this point are "socially mature" (sense of Best 1969) can be determined only through behavioral studies. Average length of males 12 layers old is about 195 cm, and average weight is about 75 kg.

The Female

Attainment of Sexual Maturity

Harrison et al. (1972) described and figured the ovaries of *S. attenuata* (as *S. graffmani*). The ovaries weigh less than 0.5 g each at birth. Weight increases gradually to about 1.5 g at about age 6 to 8 layers (average ~7 layers; an estimate of age at puberty), when there is a sudden increase in average ovary size and weight due to presence of corpora of ovulation and/or pregnancy (Figure 22). This change comes at an

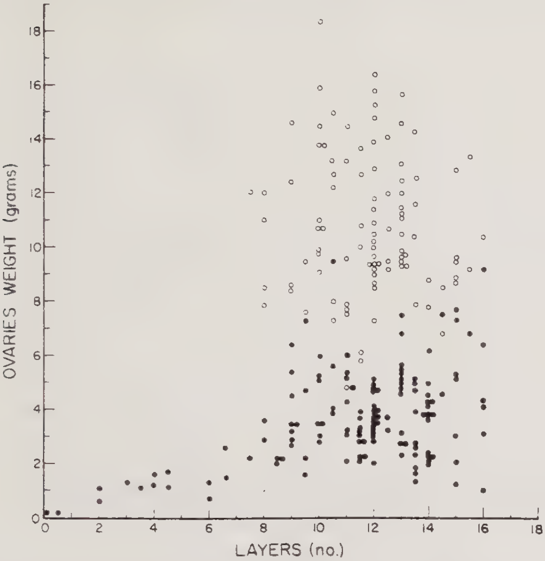

FIGURE 22.—Relationship between weight of ovaries and number of postnatal dentinal layers in *Stenella attenuata*. Open dots are females with a corpus luteum.

average total length of about 170 to 180 cm and weight of 50 to 60 kg (Figure 23).

Analysis of lengths of females with and without ovarian scars yields a more precise estimate of length at attainment of sexual maturity. The smallest of 1,410 specimens (160 cm long or longer) that possessed scars were two that were 167 cm long (one with a corpus luteum only and one with a corpus luteum and four corpora albicantia). The largest female with no scars was 193 cm long. The length-maturity curve is slightly asymmetrical, but a linear regression line through the nearly linear central portion ($M = 5.76L - 960.95$) estimates that average length at which scarring is first evident is 175.4 cm. This analysis probably underestimates length at attainment of maturity, because some of the small adults (170 to 180 cm) with many scars are those that have stopped growing at a shorter-than-average length. In other words, the left-hand portion of the frequency distribution of physically mature adults to an unknown extent artificially elevates the central portion of the length-maturity curve, making it asymmetrical.

An estimate of age and length at attainment of sexual maturity can also be derived directly from the smaller sample of females for which the number of tooth layers was determined. The youngest specimen exhibiting ovarian scarring had 7.5 layers. The oldest with no scarring had 12 layers. The estimated age at which 50% have scars is 9.14 layers ($M = 19.5t - 128.25$). Predicted length at this age is 181.6 cm (based on growth equation above). This estimate is less biased than the others above but based on much smaller samples, especially at the lower end of the layer-maturity curve.

Another estimate of length and age at first ovulation can be made by back extrapolation of a relationship between body length and number of corpora (including corpora lutea) in the ovaries (Figure 24). Length increases with corpora count until at least six to eight corpora have been accumulated, at about 183 to 190 cm. A fit of the data to the Laird growth model (above) yields the equation

$$L = 180.17 \text{ cm} \exp\{0.0541[1 - \exp(-0.2815C)]\},$$

where L = length in centimeters
C = number of corpora.

Back extrapolation of the curve to zero corpora yields an estimate of 180.2 cm. Predicted age from the growth equation is 8.74 layers.

An estimate of length at first conception can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Fifty-four primiparous females averaged 181.7 cm in length (range 167 to 193 cm). Predicted age at that length is 9.17 layers. The average length of their fetuses was 372 mm. This length is attained by about the beginning of the sixth month of gestation. Using the growth equations above to predict growth during 6 mo for the various tooth-layering models and substracting the growth increment from 181.7 cm yields estimates of length at first conception ranging from 177.7 to 180.0 cm (number 4 in Table 2). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because many females ovulate several times, and presumably continue to grow, before becoming pregnant the first time (see Ovarian Changes below).

The various methods of estimating age and length at attainment of sexual maturity yield estimates of varying accuracy (Table 2). The estimates based on tooth layers and length at first

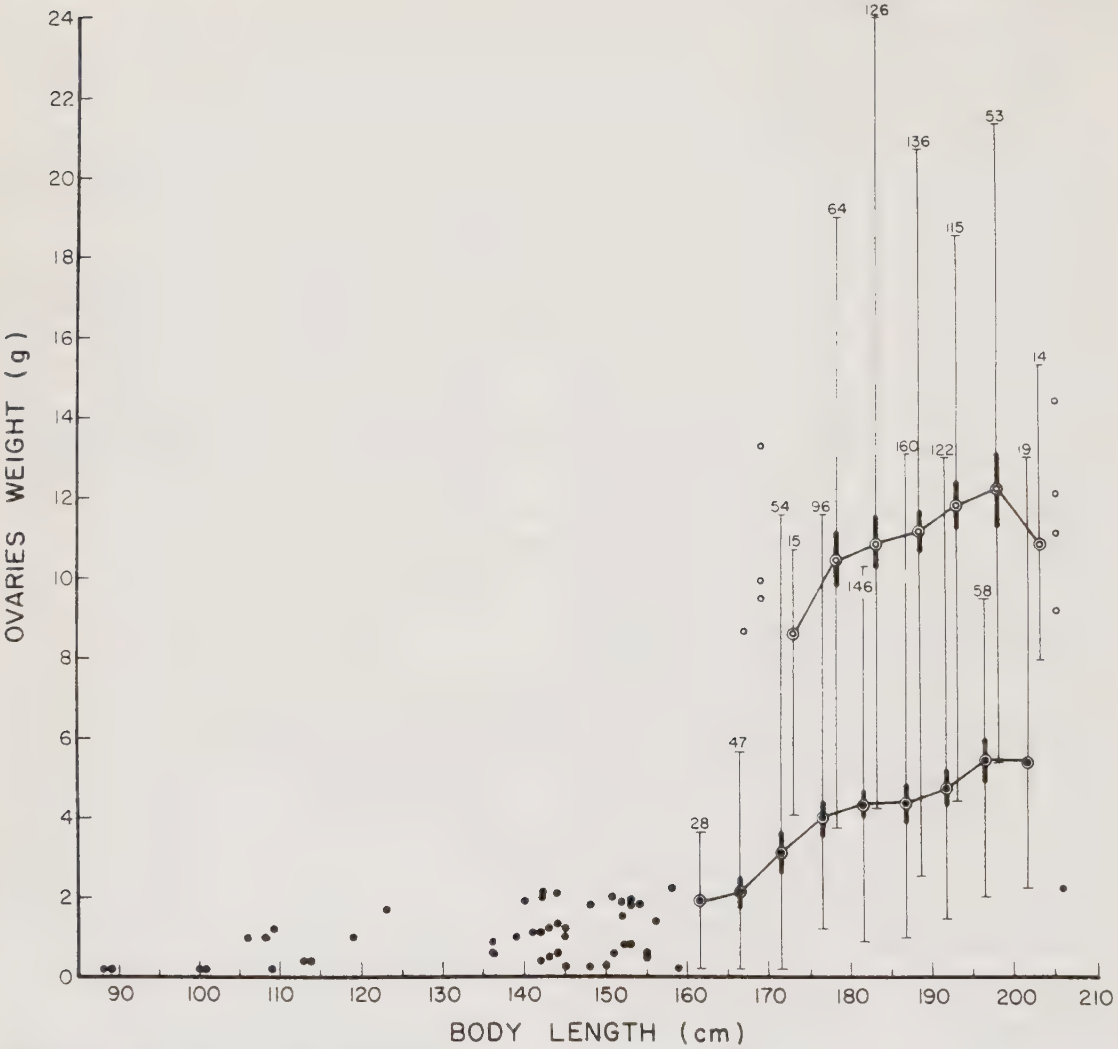

FIGURE 23.—Scatterplot of weight of both ovaries on body length in *Stenella attenuata*. Open dots represent females with a corpus luteum. For animals 160 cm or longer, where sample for 5-cm interval is 10 or more, means (circled symbols) and ranges are graphed and points are not plotted. Where the sample is ≥30, ± two standard errors are indicated by bars.

conception are the best of the four and probably bracket the true values. Under method number 3, age hypotheses numbers II and III are more probably correct than number I. Accordingly, we estimate that sexual maturity is, on the average, attained at 181 ± 1 cm and 9.0 (8.6 to 9.3) layers (5.1 to 8.3 yr, depending on the alternative layering hypothesis used).

An increase in size of Graafian follicles is another criterion of approaching sexual maturity. Diameter of the largest follicle also shows a sharp increase after 160 cm total length (Figure 25), concurrent with the increase in ovary weight (Figure 23). The largest follicle in immature females usually is less than 1 mm in diameter. The largest follicles in most ovaries containing scars are between 1 and 8 mm in diameter, but a few follicles (possibly cystic) as large as 10 to 16 mm in diameter were encountered.

Ovarian Changes in Adults

The analyses of ovarian changes are based on material collected through 1972. The corpus

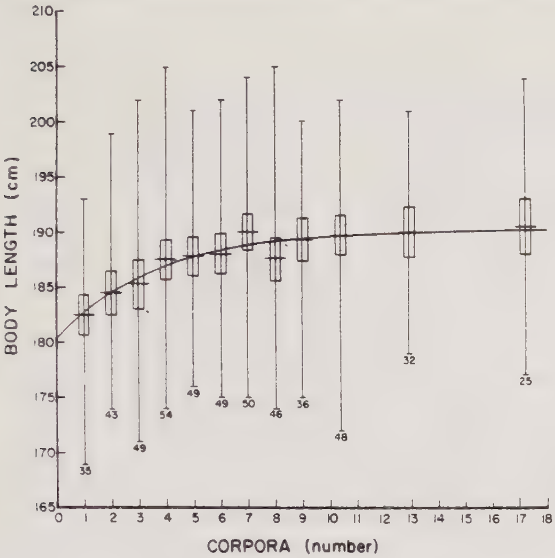

FIGURE 24.—Relationship between body length and number of corpora in *Stenella attenuata*. Average (bar), ± two standard errors (box), range (vertical line), and sample size shown.

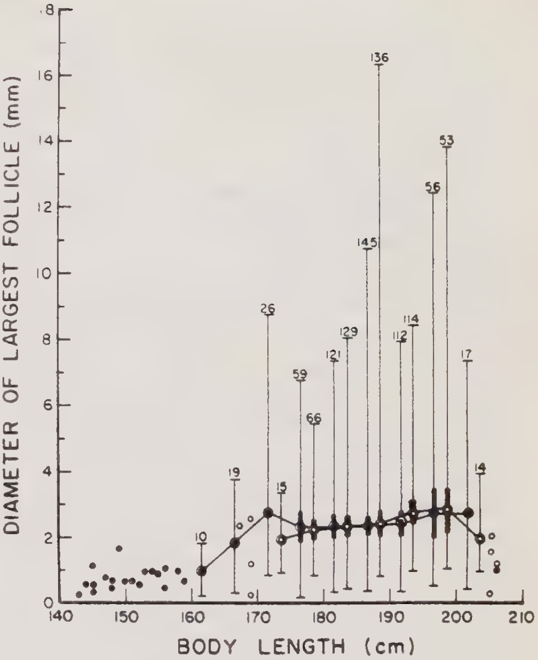

FIGURE 25.—Relationship between body length and diameter of the largest Graafian follicle in *Stenella attenuata*. Open dots represent females with corpus luteum. For length ⩾160 and $n \geqslant 10$, means (circled symbols) and ranges shown. For $n \geqslant 30$, ± two standard errors are shown. Not included are 27 "senile" specimens with follicles <0.1 mm and five juveniles 88 to 122 cm with 0- to 1-mm follicles.

TABLE 2.—Results of analyses of length and age at attainment of sexual maturity in *Stenella attenuata*, with comments (in parentheses) on pros and cons of the methods. Lengths and layer counts predicted with the growth equations are in parentheses.

Analysis	Length (cm)	Layers (no.)	Age (yr), under hypothesis I	II	III
1. Length at which 50% have corpora (probable underestimate).	175.4	(7.66)	3.8	6.7	4.3
2. Number of tooth layers at which 50% have corpora (interpolation, but small sample sizes).	(181.6)	9.14	4.6	8.1	5.6
3. Back-extrapolation of corpora-length curve (large samples, but extrapolation).	180.2	(8.74)	4.4	7.7	5.2
4. Length at first conception under hypothesis: I	177.7	(8.17)	(4.1)	—	—
II	180.0	(8.57)	—	7.6	—
III	180.0	(8.57)	—	—	5.1
(includes only those that become pregnant at first ovulation; probable underestimate).					

luteum of pregnancy arises from the ruptured follicle and has an important secretory function in maintaining early pregnancy in all mammals and full gestation in most (Amoroso and Finn 1962). The gross and microscopic structures of corpora lutea in various delphinids, including *S. attenuata,* have been described by Harrison et al. (1972).

The corpus luteum decreases in size during gestation (Figure 26). Of 242 females with corpora lutea, 229 were pregnant. Eleven with fetuses less than 20 mm long (range 1 to 20 mm) had corpora with diameters of 23 to 29 mm (average 26.0 mm, SD 2.90). The mean diameter dropped sharply to 23.6 mm (range 21 to 27 mm, SD 2.27) in 17 females with fetuses between 20 and 100 mm (using Student's *t*, means are significantly different at $\alpha = 0.01$). This amounts to about a 32% decrease in luteal volume. Size of the corpus luteum continues to decrease at a slower rate, to 22.2 mm (range 19 to 28 mm, SD 1.79) in females with fetuses 700 to 825 mm (average length at birth is 825 mm) long, a further decrease in volume of about 15%. Luteal volume in females with near-term fetuses is only about half of that shortly after conception. Mean diameter in 10 females with fetuses longer than average birth length (825 mm) was 24.0 mm (range 20 to 26 mm, SD 2.21, greater than mean for 700 to 825 mm at $\alpha = 0.01$), a volume difference of about 38% more than for fetuses 700 to 825 mm long. Delayed regression (or re-enlargement) of the corpus luteum is apparently correlated with greater-than-average length at birth.

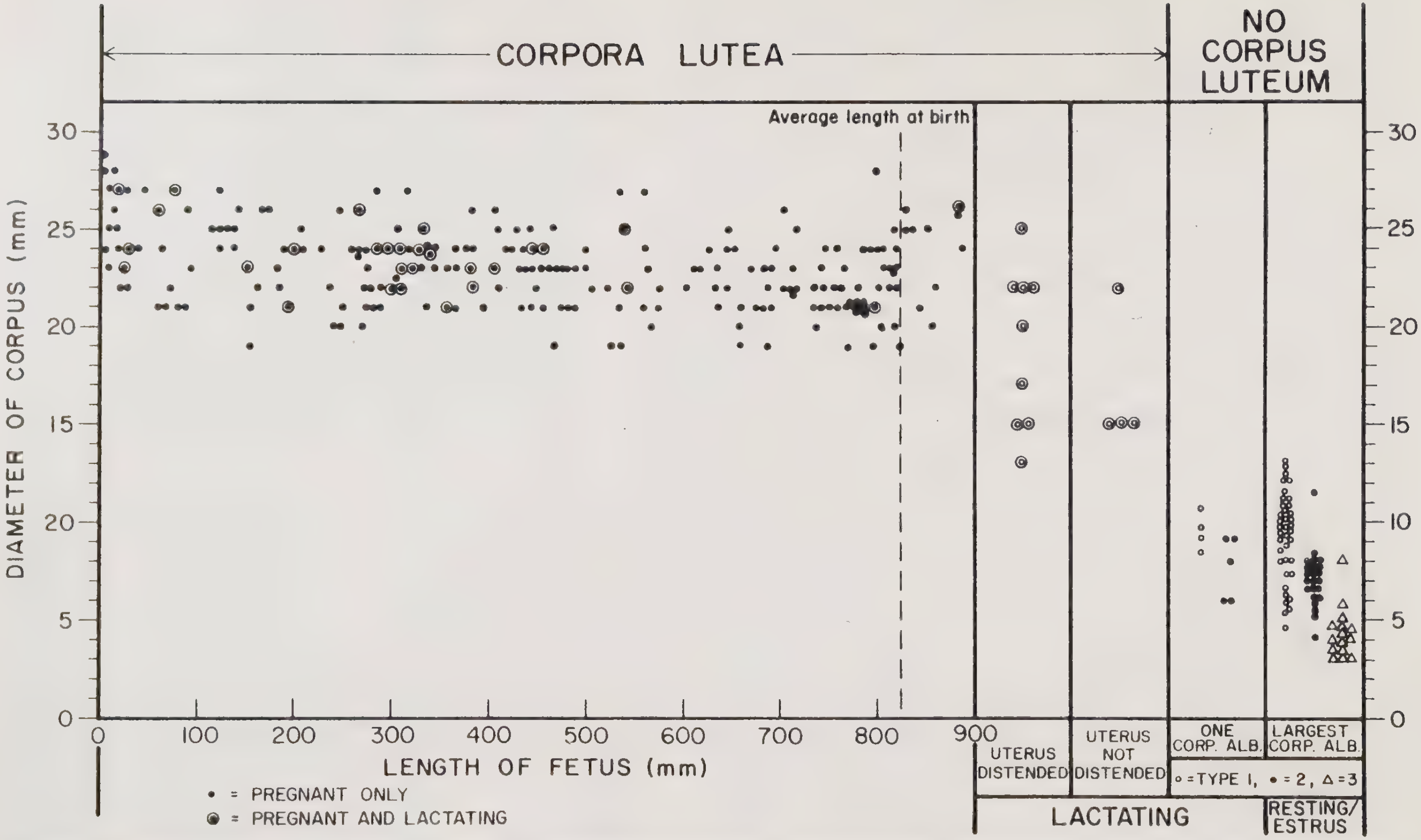

FIGURE 26.—Average diameter of corpus luteum in pregnant, lactating, and resting females of *Stenella attenuata*. Aberrant corpora (cystic, double, etc.) are not included.

Nine obviously postpartum females had corpora lutea 13 to 25 mm in diameter (Figure 26). Four lactating females with uteri not obviously distended had corpora lutea in the same size range. Average luteal volume in these lactating animals was less than half of that in animals at parturition. Some of these 13 cases may represent miscarriages.

The corpus luteum of pregnancy shrinks still further during the suckling period, losing its glandular appearance and becoming a corpus albicans. Nine of 197 lactating females without corpora lutea each had a single corpus albicans, which must represent the regressed corpus luteum of the first pregnancy. These corpora (Figure 26) were approximately spherical and 5.9 to 10.6 mm in diameter (average 8.5 mm). The lower end of this range—about 6 mm—must approximate the limit of regression during the suckling period (about 11.2 mo; see below). The small number of lactating females with corpora lutea (13) compared to the number with only copora albicantia (197) indicates that initial regression following parturition must be very rapid, perhaps occurring in less than 15 days. Still further regression in size and histological structure of the corpus albicans of pregnancy probably occurs. Many adult females have a large corpus albicans (in most cases, one of several) between 3 and 6 mm in diameter (Figure 26) with greatly degenerated structure. Unless these corpora all represent ovarian events not resulting in pregnancy, i.e., the females are all completely barren, the corpus albicans of pregnancy must decrease in diameter during a resting period following a pregnancy, to possibly as little as 3 mm.

Multiple corpora lutea are uncommon in *S. attenuata*. They were encountered in only 2 out of 258 females with corpora lutea. One of these was pregnant with twin fetuses (males, 83 and 86 mm) in the left horn of the uterus. The left ovary contained two corpora lutea of approximately equal size, each possessing a surface scar of ovulation, together with seven corpora albicantia visible on the surface. The right ovary was devoid of scars. Another female with two corpora lutea had a 592-mm fetus (male) in the left horn of the uterus. The left ovary looked very much like that of the specimen with twin fetuses, having two corpora lutea of approximately equal size and eight corpora albicantia on the surface. Neither corpus luteum bore a discernible surface scar. The right ovary was unscarred. There are two possible explanations for the presence of two corpora lutea in this specimen: 1) one of them was an accessory corpus, or 2) one of a pair of twin fetuses was aborted during early pregnancy. In any case, the incidence of multiple corpora lutea is very low in *S. attenuata,* less than 1% in the sample examined. This is in sharp contrast to some other cetaceans, in which rates of presence of accessory corpora range to 15.6% (*Delphinapterus leucas* —Brodie 1972). The contribution of double and accessory corpora lutea to the accumulation of corpora albicantia can be considered to be negligible in *S. attenuata.*

Corpora albicantia in *S. attenuata* represent both regressed corpora lutea of pregnancy and regressed corpora of ovulations that do not result in pregnancy. This conclusion is based on the accumulation rate of corpora albicantia and on the estimate of the mean length of the calving interval (see below). We were not, however, able to differentiate between small regressed corpora lutea and regressed corpora of ovulation. This impasse, also encountered by workers dealing with other cetaceans (Harrison et al. 1972) is caused by the wide and largely discordant variation in size, shape, surface texture, and internal structure and color of the corpora albicantia. If one looks at enough corpora, it is possible to find corpora with these characters in almost any combination of expressions.

Harrison et al. (1972) found no more than six corpora albicantia in the ovaries of any *Stenella* female. In the present sample, however, nearly half (44%) of the females had more than six corpora, including the corpus luteum. Fifty-five females of 1,131 had 15 or more corpora; one had 28 (Figure 27). Three thousand five hundred and two corpora from ovaries of 530 females were scored to six categories. These categories are somewhat arbitrary in view of the continuity of regression and the wide variation discussed above, but, nonetheless, they are useful in analyzing the course of regression. The numbers and proportion of total corpora complement represented by each of these categories varies with the total number of corpora (Table 3, Figure 28). The categories were defined as follows:

Type 1. Surface raised, smooth or slightly wrinkled. Looks externally like a small corpus luteum. Cortex white or yellow, with obvious remnants of vascularization. Center solid or loosely constructed, consisting mainly of white

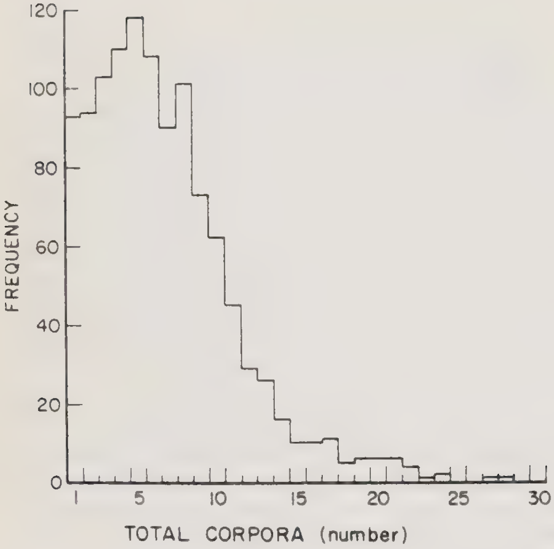

FIGURE 27.—Frequency distribution of corpora count in 1,131 females of *Stenella attenuata*.

connective tissue, 3.5 to 15.5 mm in diameter, average 7 mm. These corpora almost certainly are nearly all regressed corpora lutea. Four hundred fifty-six were encountered (13.2%). Females with two or more corpora have, on the average, about one Type 1 corpus (Figure 28), although as many as five may be present (Table 3).

TABLE 3.—Types of corpora present in ovaries of *S. attenuata* in relation to total corpora. Averages in Figure 28.

Total number of corpora (including corpora lutea)	Sample size (no.)	Range of number of each type of corpus albicans—Type:					
		1	2	3	4	5	6
1	35	0-1	0-1	0	0	0	0
2	42	0-2	0-2	0-1	0-1	0-1	0
3	48	0-3	0-3	0-2	0-1	0	0
4	53	0-3	0-4	0-3	0-1	0-2	0
5	49	0-5	0-4	0-5	0-2	0-2	0
6	49	0-5	0-4	0-6	0-3	0-1	0
7	50	0-5	0-5	0-6	0-3	0-2	0-1
8	46	0-5	0-6	0-7	0-2	0-4	0
9	36	0-2	0-5	2-9	0-4	0-3	0-1
10-11 (average 10.4)	48	0-4	0-5	3-10	0-2	0-2	0-1
12-14 (average 12.9)	32	0-2	0-5	3-14	0-3	0-4	0-3
15-27 (average 17.2)	25	0-4	0-5	7-19	0-2	0-9	0-1
Total	513	0-5	0-6	0-19	0-4	0-9	0-3

Type 2. Surface raised and wrinkled. Interior white to yellow, often with traces of luteal cortex and vascularization. Center solid or loosely constructed, consisting mainly of white connective tissue. Definitely less integrated in structure than Type 1 (above). Diameter 3.0 to 12.0 mm, average 6 mm. The evidence on accumulation rate (below) suggests that these corpora are probably a mixture of regressed corpora lutea and corpora of ovulation. We found 787 of this type (22.5%). The number of Type 2 corpora is relatively constant in females with three or more corpora, at about one and one-half (Figure 28) with a

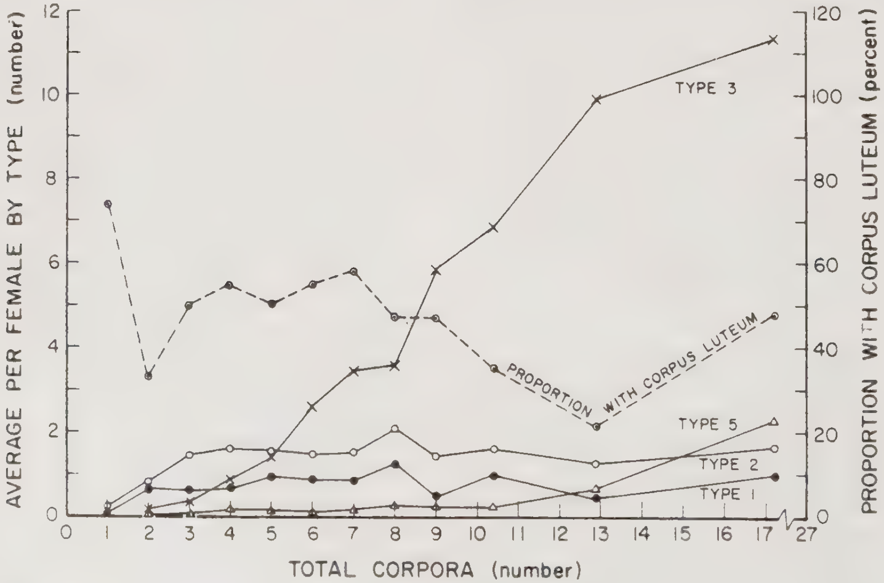

FIGURE 28.—Relationships between numbers of corpora of various types and total number of corpora in ovaries of females of *Stenella attenuata*. Ranges and sample sizes in Table 4.

range of 0 to 6 (Table 3). This number is tightly correlated with the number of Type 1 corpora (Figure 28), indicating that there may be some overlap in the classification criteria for these categories.

Type 3. Surface usually not raised; scar usually smaller than Type 2 and heavily wrinkled. May be pedunculate and flattened. May be flattened against the surface or may run deep into the ovary. Interior consists of white connective tissue. May have yellow "stains" around the white center. When many corpora are present, some of this type may be present but not apparent at the surface. Diameter 2.0 to 8.5 mm, average 3.5 mm. This is a catch-all category for all small compact corpora with surface scars and internal structure. It probably includes both regressed corpora lutea and corpora representing ovulation and other events. We found 1,999 corpora of this type (57.1%). The number increases steadily with total corpora number (Table 3, Figure 28), while the numbers of Types 1 and 2 corpora remain constant, indicating that Types 1 and 2 corpora regress into and accumulate as Type 3 corpora. This is assuming, of course, that total corpora count is related to age (see below).

Type 4. Thin, flattened against the surface of a new corpus luteum. Two to 15 mm in diameter. These are Types 2 and 3 corpora that cannot be allocated to those categories because of distortion caused by the corpus luteum. One hundred were encountered (2.9%).

Type 5. Surface trace very slight or apparently absent. Interior deep yellow or orange, with no concentrated connective tissue or apparent internal structure. Diameter 0.5 to 5.5 mm, average 2 mm. Harrison et al. (1972) have suggested that this type of corpus is the end result of regression of an atretic lutealized follicle. We encountered 149 (4.3%).

Type 6. A small surface scar with no discernible internal structure. Two to 5 mm in diameter. Only 11 corpora of this type were encountered (0.3%). They may represent extremely regressed corpora of other types or may originate from different ovarian events.

Types 1, 2, and 3 comprise a series of increasing regression and/or decreasing complexity of original structure, and it is probable that regressing corpora lutea pass through these types or stages. The shapes of the diameter frequency distributions (Figure 29) suggest that corpora albicantia regress to an average size of about 3 mm in diameter and then persist and accumulate at that size for at least part of the remainder of the life of the female. The skewness of the aggregate distribution (sum Types 1, 2, and 3 in Figure 29) becomes even more significant when one considers that the volume of the corpus decreases as the cube of the diameter. On a volume scale, the left

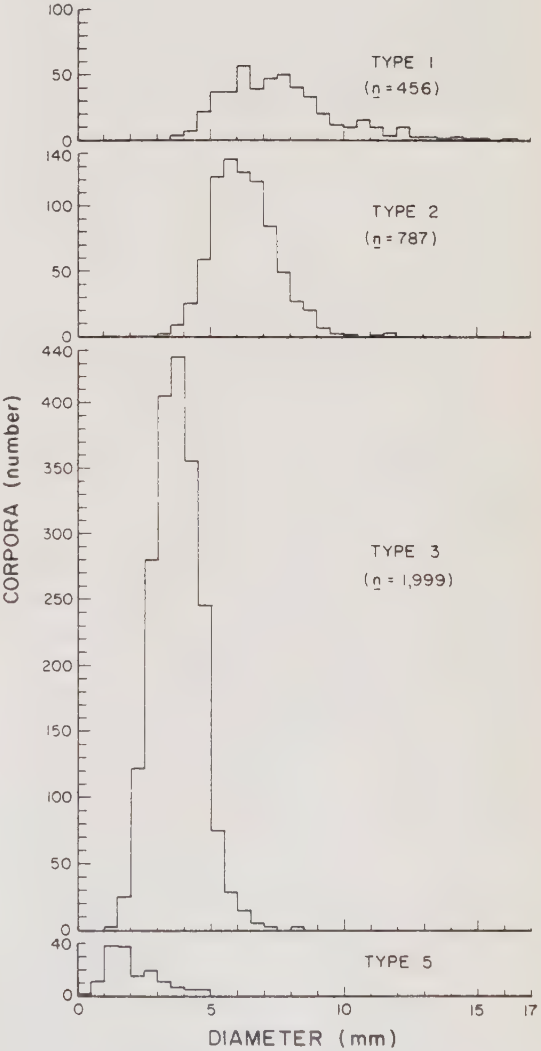

FIGURE 29.—Frequency distribution of diameter of Types 1, 2, 3, and 5 corpora albicantia in *Stenella attenuata*.

side of the curve would be steeper and the right side less steep.

Consideration of the relative rates of deposition of corpora in the left and right ovaries is important to the question of persistence of corpora. The distribution of corpora between left and right ovaries is related to the number of corpora present (Table 4). The first corpus occurs in the left ovary about 94% of the time. Subsequent corpora occur in the same ovary as preceding ones at about the same rate (~95%), causing a gradually increasing percentage of animals with corpora in both ovaries, until about 10 to 11 corpora have been deposited, when emphasis switches sharply to the opposite ovary (left or right). All females with 15 or more corpora (27 specimens) had corpora in both ovaries.

TABLE 4.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 488 specimens of *Stenella attenuata*.

Corpora (no.)	Sample size (no.)	Location of corpora		
		Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	31	93.6	6.4	—
2	40	85.0	7.5	7.5
3	44	86.5	4.5	9.0
4	53	88.7	1.9	9.4
5	47	78.8	2.1	19.1
6	48	75.0	4.2	20.8
7	45	73.4	2.2	24.4
8	41	61.0	2.4	36.6
9	34	70.6	2.9	26.5
10-11	47	46.8	2.1	51.1
12-14	31	6.5	0.0	93.5
15-27	27	0.0	0.0	100.0
Total	488			

A group of 15 seemingly postreproductive females was encountered. These specimens had very small, obviously regressed ovaries with 10 to 15 Type 3 or smaller corpora albicantia (Figure 30). They had no corpora lutea or Type 1 corpora

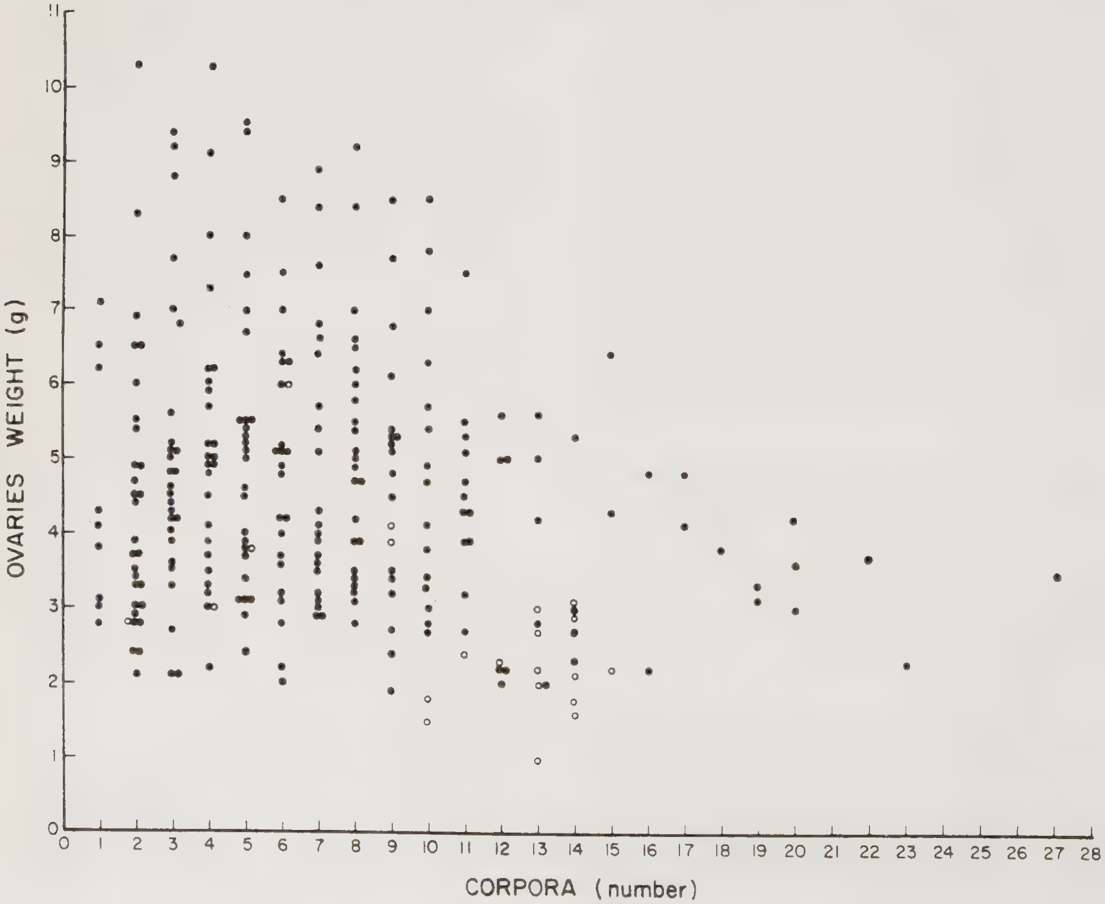

FIGURE 30.—Scatterplot of ovaries weight on number of corpora in *Stenella attenuata*. Females with corpus luteum not included. Open dots are females with no Type 1 or 2 corpora albicantia.

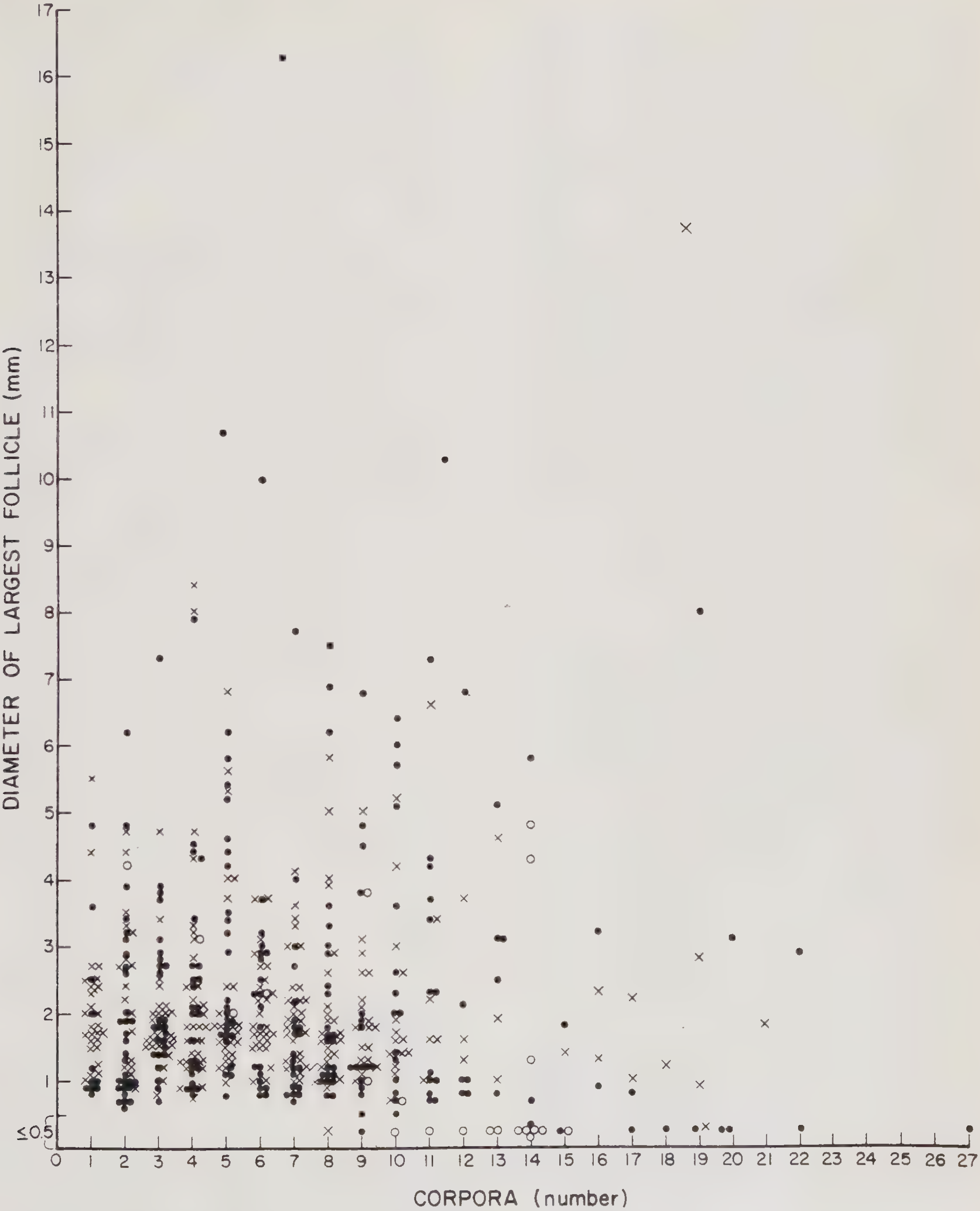

FIGURE 31.—Scatterplot of diameter of largest follicle on number of corpora in *Stenella attenuata*. Females with corpus luteum indicated with ×. Open dots are females with nor corpus luteum or Type 1 or 2 corpora albicantia.

albicantia. They also typically had very small Graafian follicles (Figure 31). A consideration of these females bears on the question of persistence of corpora albicantia. Sergeant (1962) encountered similar females in *Globicephala*. They comprised about 5% of adult females. He called them "senile" and concluded that the ovarian scars in these animals represent some residual subset of the maximum complement of corpora of pregnancy, ovulation, and other events. He implied that they probably are the corpora of pregnancy, since those corpora are larger at the outset and presumably less likely to regress to the point of macroscopic disappearance. The ovarian data for *S. attenuata* do not support this hypothesis of disappearance of some corpora in regressed ovaries. The regressed ovaries have 10 to 15 corpora (Figures 30 and 31). The ovaries of other, still reproductive females are larger and have 16 to 27 corpora, although follicles are typically smaller than in reproductive females with fewer corpora (Figure 31). Three alternative hypotheses explain this apparent dichotomy in females with 10 or more corpora:

1. The usual maximum number of corpora is about 21, and some corpora disappear in postreproductive females, i.e., the "senile" group in Figure 30 properly belongs at the far right side of the plot at the end of a downward trend in ovary weight (the hypothesis of Sergeant 1962).
2. Corpora are laid down at about the same rate in all individuals, but some become postreproductive at about 10 to 15 corpora while others continue to accumulate corpora (16 to 27) until a greater age, i.e., the corpora scale in Figure 30 is effectively an age scale. Under this hypothesis, corpora do not disappear.
3. Corpora are accumulated at rates varying widely among individuals, but the typical maximum complement is 10 to 15 corpora, i.e., the reproductive females with more than 15 corpora in Figure 30 properly belong in the body of the distribution in the left two-thirds of the plot. A possible explanation for widely varying rates of accumulation is that some females are more fecund and the senile period is reached with some maximum number of pregnancies, so that the varying ratios of corpora of pregnancy to corpora of ovulation may produce the apparent dichotomy. Sergeant (1973) found greatly varying individual rates of ovulation in the white whale, *Delphinapterus leucas*.

In order to examine these alternative hypotheses, the females in Figure 30 and 31 with 10 or more corpora were examined in three groups—A, B, and C:

A. 10 to 15 corpora, reproductively active (corpus luteum and/or Types 1 and 2 corpora albicantia).
B. 16 or more corpora, reproductively active.
C. 10 to 15 corpora, postreproductive (ovaries regressed, no corpus luteum or Types 1 or 2 corpora albicantia).

The three groups were compared in terms of corpora count, weight of ovaries, size of largest follicle, number of dentinal layers, total length, and relative corpora counts in left and right ovaries (Table 5). Only nonpregnant females were included in the sample for ovary weight. Follicle size was examined separately for pregnant and nonpregnant animals.

Ovary weight and follicle size for nonpregnant animals decline progressively from A to C. This is

TABLE 5.—Characteristics of females of *Stenella attenuata* in groups A, B, and C (see text).

Item	A	B	C
Corpora (no.)			
Sample size	67	24	15
Average	11.2	18.9	12.9
Range	10-15	16-27	10-15
SD	1.41	2.56	—
Ovary weight (g) (nonpregnant)			
Sample size	44	13	15
Average	4.4	3.6	2.2
Range	2.0-8.5	2.2-4.8	1.0-3.1
SD	1.61	0.81	0.59
Largest follicle (mm) (nonpregnant)			
Sample size	27	13	<14
Average	2.9	1.5	<0.5
Range	<0.5-10.3	<0.5-8.0	0.5-4.3
SD	2.53	2.35	—
Layers (no.)			
Sample size	30	18	7
Average	13.1	13.1	13.2
Range	10.0-16.0	11.0-15.0	11.5-16.0
SD	1.39	1.31	1.52
Length (cm)			
Sample size	67	24	15
Average	190.1	190.3	187.0
Range	172-202	177-204	179-192
SD	6.43	6.78	3.54
Left/right ovary			
Sample size	65	23	15
Average in right (%)	24	33	29
Left/right (no./no.)	548/178	291/144	—

a requirement of hypothesis 1, above, but does not eliminate hypotheses 2 and 3.

The three groups do not differ in average estimated number of tooth layers. This may, in part, be due to the difficulty of accurately counting the innermost layers in teeth with more than 12 layers (the number of layers is probably underestimated by as much as one-third in teeth with large amounts of convoluted secondary dentine), but careful comparison of the teeth of the three groups in terms of other features presumably correlated with age, such as tip wear, degree of closure of the pulp cavity, and amount of secondary dentine does not indicate that any group is older than any other. This evidence is against hypothesis 1, which requires that group C be older than A, and hypothesis 2, which requires that B be older than A and C.

Groups A and B have reached asymptotic length (~190 cm). The animals in group C averaged about 3 cm less. A statistical comparison of A with B using Student's t indicates that the difference is significant at $\alpha = 0.05$. These results do not eliminate or support directly any of the hypotheses. Since A, B, and C are about the same age, the length data indicate that asymptotic length may be less for females that become senile with 10 to 15 corpora. This indirectly supports the idea of considerable individual variation in life history.

The most convincing evidence against hypothesis 1 has to do with number of corpora in right versus left ovaries. If the emphasis in corpus deposition shifts from left to right at about 10 corpora, and if group C regresses from group B (animals with about 20 corpora) losing about 6 corpora in the process, then group C should have about equal numbers of corpora in the right and left ovaries. If most corpora of ovulation come in early reproductive life (as data analyzed below indicate) and, as suggested by Sergeant (1962), are more likely to disappear than corpora of pregnancy because of smaller initial size, then the regressed group C should have, on the average, more corpora on the right than on the left, because most of the corpora of pregnancy would be in the right ovary. Forty-one percent of the corpora in 14 individuals having 18 to 22 corpora (average 19) were on the right. Only 29% of the corpora in group C were on the right. The difference between C and A (29 and 24%) can be accounted for simply by the difference in average total corpora count (12.9 and 11.2). These results eliminate the hypothesis (number 1 above) of loss of corpora with regression of ovaries.

The various lines of evidence largely speak against hypotheses 1 and 2 and support hypothesis 3, that of great individual variation in life history and of persistence of corpora albicantia. This is in line with findings by some other workers in small cetaceans (Sergeant 1962, 1973; Brodie 1971).

The data on the relationship of percent occurrence of corpora lutea to number of corpora (Figure 28) also support the hypothesis of widely varying rate of accumulation of corpora albicantia. After stabilization at about 50% at 3 to 4 corpora, the rate declines after 8 to 9 corpora to 20% at 13 corpora; but the rate for females with 17 to 27 corpora is again 50%. Assuming that fecundity is inversely related to age, this pattern suggests that the females in the 17 to 27 group are about the same age as those in the 3 to 9 group.

Ovulation Rate

Even assuming that corpora albicantia persist and represent various ovarian events, estimating average rates of accumulation is difficult because of 1) the above-mentioned unreliability of age estimates based on more than 12 tooth layers, 2) the evident individual variation in accumulation rate, and 3) change in ovulation rate during the reproductive span. All of these factors must contribute to the scatter in a plot of corpora number (including corpus luteum) on estimated age (Figure 32). Several workers have pointed out that cetacean ovaries often contain two or more corpora of the same size and same stage of regression. It has been suggested that these are the result of multiple infertile ovulations or luteali-zation of atretic follicles in newly mature animals (Harrison et al. 1972). Many in the present series of ovaries had two or more corpora (of Type 1 or 2) that were very similar in size and structure and must have resulted from nearly contemporaneous events. One probable multiple ovulation is apparent in Figure 32. This female, field number CWOR8, possessed 7 or 8 well-defined layers in its teeth. In spite of its extreme youth, it had a small corpus luteum, three Type 1 corpora, two Type 2 corpora, one Type 3 corpus, and one Type 4 corpus. The uterus was empty, and there was no milk in the mammaries. The animal could not have been reproductively active for more than about a year, but had already experienced eight

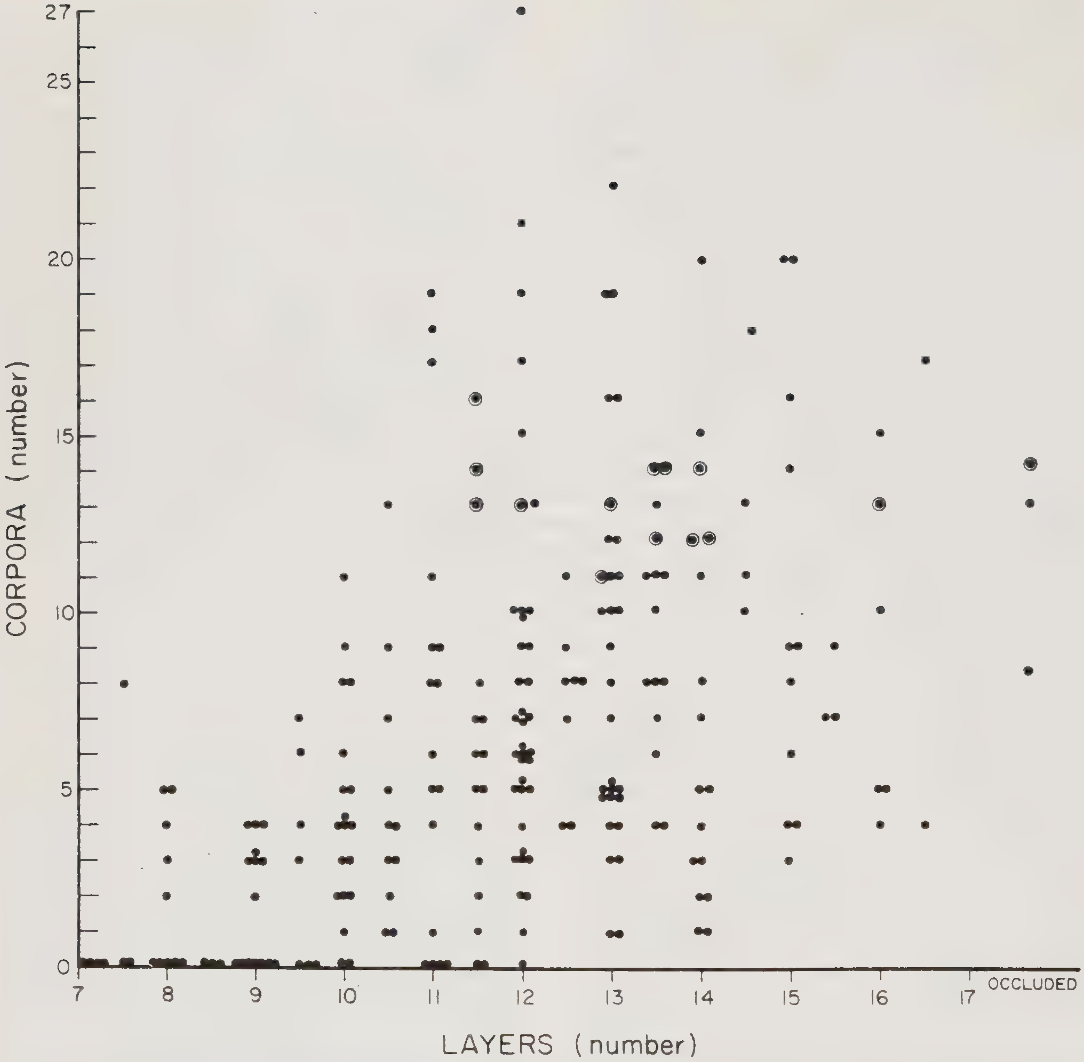

FIGURE 32.—Scatterplot of number of corpora on number of postnatal dentinal layers in *Stenella attenuata*. Circled symbols are senile females (shriveled ovaries with no corpus luteum or Type 1 or 2 corpora albicantia).

apparently nonreproductive ovarian events that resulted in corpora belonging to all of the types through which a corpus luteum must pass during regression to a small corpus albicans.

Calculation of average ovulation rates from the data in Figure 32 must take into account individual variation in age at first ovulation. The females in Figure 32 were grouped into 10 one-layer intervals beginning with 7.5 layers (Table 6). The average reproductive age in interval p was calculated as

$$\bar{A} = \left(\sum_{i=1}^{p} a_i b_i \right) \div c,$$

where a_i = % maturing in ith interval (% mature in i minus % mature in i - 1)

b_i = average reproductive age in interval p of females mature in i

c = % mature in interval p.

Average reproductive age in the ith interval of

TABLE 6.—Average reproductive ages and corpora counts of females of *Stenella attenuata* used in estimating ovulation rate based on corpora and tooth layers.

Layers (no.)	Sample (no.)	Proportion mature (%)	Average reproductive age of mature (layers)		Average corpora (no.)	
7.5- 8	13	46.2	0.50	1.43	4.50	4.21
8.5- 9	18	44.4	1.56		3.25	
9.5-10	24	79.2	1.67		4.53	
10.5-11	25	84.0	2.56		6.42	
11.5-12	52	94.2	3.25		8.35	
12.5-13	36	100.0	4.05		8.92	
13.5-14	31	100.0	5.06		8.71	
14.5-15	15	100.0	6.07	6.60	10.87	10.45
15.5-16	7	100.0	7.08		9.86	
>16	3	100.0	8.09		9.75	
Total	224					

Note: Teeth of all available females with more than 12 corpora were sectioned, while only a nonselective subsample of females with fewer corpora were included. The effect on estimate of average reproductive age is negligible, since nearly all had 11 or more layers.

females maturing in *i* was set at 0.50 layers. Because of small sample sizes, the first three intervals and the last three were pooled. The results show an increase in average corpora count (number of ovulations) with reproductive age (Figure 33). A curvilinear fit to the interval means, using a power model forced through the origin, fits well and indicates that ovulation rate is higher in animals of reproductive age 0-2 layers than in older animals. The breaking point seems to come at about 12 layers, when about 6 corpora have been accumulated and rate appears to become nearly constant. Average ovulation rates estimated from the curve are about four during the first layer, two during the second, and about one per layer thereafter.

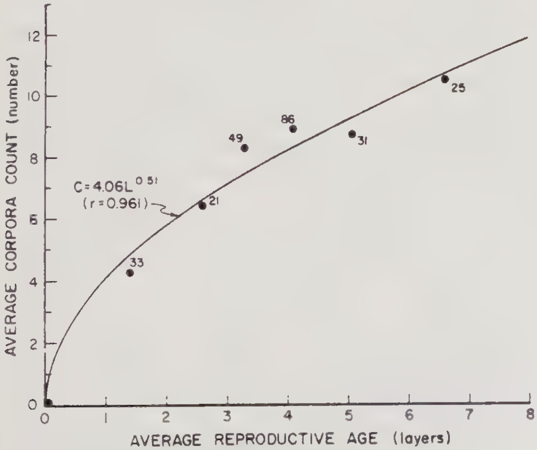

FIGURE 33.—Relationship between average number of corpora and average reproductive age (in layers) in *Stenella attenuata*.

Calving Interval

The pattern of reproduction definable with the methods used here consists of three phases: pregnancy, lactation, and a period of inactivity and/or estrus called here "resting/estrus." The length of pregnancy was estimated above as 11.5 ± 0.2 mo. We estimated length of lactation in three ways, based on 1) stomach contents of calves, 2) numbers of lactating females and calves, and 3) ratio between numbers of lactating and pregnant females.

The forestomachs of 45 calves less than 150 cm long were opened and examined by eye for presence of milk. Twenty-one were empty. The stomachs of four calves 120 to 130 cm long contained both milk and solid food (fish and/or squid). Stomachs of 8 smaller calves (80 to 115 cm) contained only milk, and 12 of the larger calves (130 to 150 cm) apparently contained only solid food. About 130 cm appears to be the length at which effective weaning occurs. The estimated time required to grow to 130 cm is 9.4 mo (based on growth curve above). This estimate is not very reliable for two reasons: the sample is small, and small amounts of milk could be present and undetectable by eye, i.e., suckling could continue at a low level after the effective shift to solid food. The estimate can, however, be considered to be a probable lower bound on length of lactation.

A second estimate is based on the assumptions that 1) a suckling calf exists for each lactating female and 2) the samples of specimens are unbiased with respect to suckling calves and lactating females. Given these assumptions, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning. This length in eight variously sized, 1-mo "random" samples of calves and females ranged from 125 to 145 cm (Table 7). The aggregate estimate for the eight samples pooled (320 lactating females) is 137 cm. Average age at 137 cm is estimated at 1.94 tooth layers, or (assuming two layers accumulated during first year) 11.6 mo. If calves were overrepresented in the samples, this would be an underestimate. If they were underrepresented, it would be an overestimate. It would be an overestimate if the assumption that the number of lactating females equals the number of nursing calves were not valid. The assumption is not valid if the mortality of nursing calves is

TABLE 7.—Length at which cumulative frequency of calves equals the number of lactating females in eight 1-mo samples of *Stenella attenuata*.

Sample (mo)	Lactating females (no.)	Length (cm) at which cumulative frequency of calves = no lactating females
Oct. 1972	51	132
Jan. 1973	65	125
Feb. 1973	50	144
Mar. 1973	48	136
Apr. 1973	13	142
May 1973	32	142
June 1973	18	145
Nov. 1973 (Oct. 28-Dec. 11)	43	142
Total	320	137

higher than that of lactating females and lactation continues after death of a nursing calf.

A third estimate of length of lactation was derived from the ratio of lactating to pregnant females. This analysis included all the material from 1971 and 1972, when only adult females were sampled, as well as the material included in the calf-lactating female analysis above. Females both lactating and pregnant were included in both categories. The assumption is made that samples were unbiased with respect to relative representativeness for lactating and pregnant females. The ratio was 0.95 in the 1971 sample (86 adult females), 1.00 in 1972 (455), 0.96 in 1973 (573), and 0.97 for the pooled samples (n = 1,114; Table 8). The ratio of lactating to pregnant should equal the ratio of the lactation period to the gestation period. Gestation is 11.5 mo, therefore lactation is by this method estimated at 0.97 times 11.5 mo, or 11.2 mo. Estimated length at this age is 135.5 cm.

The three estimates of 9.6, 11.6, and 11.2 mo are based on largely independent assumptions and are close enough to each other to indicate that length of lactation is almost certainly between 9 and 12 mo. Of the three, the central estimate, 11.2 mo, is best in terms of sample size and probable validity of assumptions and is used below in estimating length of the calving interval.

The basic data used for estimating average length of calving interval were the relative frequencies of adult females in several reproductive conditions (Table 8). Adult females were defined as those with at least one corpus luteum or corpus albicans. Senile females were those with 10 or more corpora albicantia, no corpus luteum or Type 1 or 2 corpora albicantia and ovaries weighing less than 3.5 g. Resting/estrus females were those nonsenile adults that were neither pregnant nor lactating. Many of these (16 to 31%) had a corpus luteum. The corpus luteum may have represented an undetected very early pregnancy, a very recently aborted pregnancy, loss of a calf shortly after birth (resulting in cessation of lactation), or may have been a corpus luteum of ovulation. All of these alternatives may be represented in the samples.

In calculating the proportions of females in the three phases of pregnant, lactating, and resting (Table 9), senile females were excluded. One-half of the animals simultaneously pregnant and lactating were assigned to the pregnant category and one-half to the lactating category.

The average length of calving interval was estimated by two methods — 1) using the estimates of gestation and lactation periods and 2) using the percentage of females pregnant. The data for the 3 yr are comparable (Table 9), with the exception of possible existence of a trend in proportion resting; therefore, length of calving interval was estimated from the pooled data. Eighty-four and one-half percent of reproductive females were pregnant or lactating. Pregnancy (11.5 mo) plus lactation (11.2 mo) total 22.7 mo. If the proportion in a phase is equal to the proportion of the total

TABLE 8.—Reproductive condition of 1,114 adult female specimens of *Stenella attenuata*, collected 1973.[1]

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant only (P)	31	36.0	180	39.7	233	40.7	444	39.6
Lactating only (L)	29	33.7	180	39.7	223	38.9	432	38.8
Pregnant and lactating (PL)	13	15.1	16	3.5	17	3.0	46	4.1
Resting/estrus $\left(\frac{A}{B}\right)$ (R)	11 $\left(\frac{3}{8}\right)$	12.8	64 $\left(\frac{10}{54}\right)$	14.1	94 $\left(\frac{29}{65}\right)$	16.4	169 $\left(\frac{42}{127}\right)$	15.2
Senile[2]	2	2.3	15	3.3	6	1.0	23	2.1
Total	86	100	455	100	573	100	1,114	100

[1] In the resting/estrus category, subcategories A and B (in parentheses) are specimens with and without a corpus luteum, respectively

[2] ≥10 corpora, no Type 1 or 2 corpora, and ovaries ≤ 3.5 g.

TABLE 9.—Proportions of 1,091 adult reproductive females of *Stenella attenuata* in pregnant, lactating, and resting/estrus phases.

	1971		1972		1973		Total	
	No.	%	No.	%	No.	%	No.	%
Pregnant (P + ½PL in Table 8)	37.5	44.6	188	42.8	241.5	42.6	467	42.8
Lactating (L + ½PL)	35.5	42.3	188	42.8	231.5	40.8	455	41.7
"Resting" (R)	11	13.1	64	14.4	94	16.6	169	15.5
Total reproductive females	84	100	440	100	567	100	1,091	100

calving interval spent in that phase, then total length of the interval cycle is 22.7 mo divided by 0.845, or 26.9 mo.

A second estimate was obtained directly from the proportion of females pregnant. In calculating this proportion, all pregnant animals were included (P + PL in Table 8): 490 of 1,091 reproductive females were pregnant, or 44.9%. Division by length of pregnancy, 0.958 yr (11.5 mo), yields an estimate of annual pregnancy rate, 0.469. The reciprocal of pregnancy rate, 2.133 yr, or 25.6 mo, is an estimate of average length of calving interval.

Both estimates of length of calving interval, 26.9 and 25.6 mo, are overestimates to the extent that the "resting" females with corpora lutea represented uncounted pregnancies, but the effect can be at most very minor. For example, if all these females represented undetected pregnancies or pregnancies aborted during capture, the unlikely extreme case, the estimates would be 25.7 and 24.7 mo respectively, an average difference of about 1 mo. Since the "resting" females with corpora lutea probably represent a mixture of causes and conditions, including nonfertile ovulations, the probable effect on the estimates is less than 1 mo. Considering this factor and the closeness of the two estimates to each other, it seems certain that the true length of the interval is between 24 and 27 mo. The lower of the two estimates, which is based on fewer assumptions and calculations, was rounded off to 26 mo and is used below in further analysis of life history. The average pattern of events then, consists of 11.5 mo of pregnancy, 11.2 mo of lactation, and 3.3 mo of resting and/or estrus.

Overlapping Lactation and Pregnancy

About 9.6% of lactating females were also pregnant (Table 8). Most had fetuses less than 35 to 40 cm long (Figure 26), about halfway through the gestation period. This suggests that overlap when it occurs is usually about 5 to 6 mo long, i.e., conception occurs about halfway through the lactation period of about 11 mo, making the calving interval about 20 mo long instead of 26. The very few lactating females with near-term fetuses may have conceived during postpartum estrus or may have begun to lactate shortly before parturition.

The data on Graafian follicles are consistent with the theory that postpartum estrus occurs during lactation (Figure 34). The largest follicle in the ovaries of resting/estrus females (including those presumably about to ovulate) is on the average 3 to 4 mm in diameter. After ovulation and conception, the remaining large follicles regress rapidly to about 2 mm (or become lutealized or atretic). There is a further net decline during gestation to about 1.5 mm, and during lactation the main modal diameter is about 1.0 mm. During both pregnancy and lactation, however, about 10% of the females (excluding senile individuals, as defined above) have follicles that are within the size range (≥3.0 mm) of the presumably ripe follicles present during the resting/estrus phase. This is most clear-cut during lactation. Most of the larger follicles during pregnancy occur in females having fetuses 400 to 500 mm long, or about halfway through the gestation period (Figure 34).

Decrease in Reproductive Rate with Age

Reproductive rate decreases with age. Age-specific estimates of pregnancy rates and lactation rate were calculated from a random sample of the data for specimens for which teeth were sectioned (stratified to insure representation of corpora-number strata in about the proportions as in the entire sample). The analysis shows decline of pregnancy rate from about 0.6 at 8 to 9 layers to about 0.3 at 16 to 17 layers (Figure 35). The weighted rate for the pooled sample of 138 used in the calculation was 0.51, comparable to the rate of 0.47 obtained for 1,091 animals (above). The specimens for which teeth were sectioned were about one-third from 1971 and two-thirds from 1972, with a few specimens from earlier years. Lactation rate

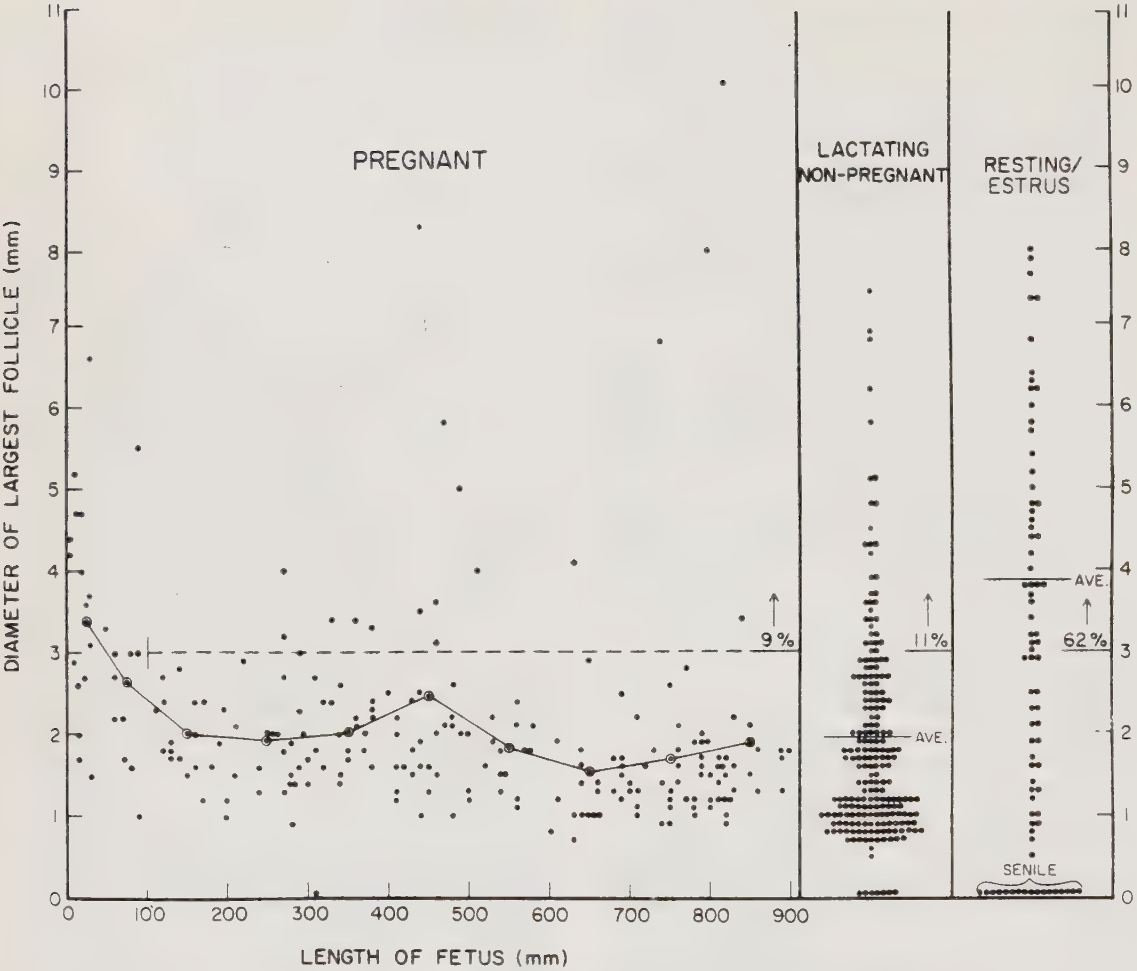

FIGURE 34.—Diameter of largest follicle in pregnant, lactating, and resting females of *Stenella attenuata*.

(Figure 35) increases from about 0.1 at 8 layers to about 0.6 at 12 layers and then again decreases to about 0.5.

The initial very low lactation rate compared to pregnancy rate, of course, reflects the fact that a very high percentage of the young females are pregnant for the first time and thus cannot be lactating. The lactation rate climbs rapidly to a level about equal to the pregnancy rate (at about 12 layers) and behaves like the pregnancy rate thereafter. The apparent decline of reproductive rates in older females may be related to the physiological or social mechanisms that cause the appearance of postreproductive females in this age group (see above; not included here).

Sex Ratios

The overall sex ratio was 44.9% males and 55.1% females (Figure 36). Many large samples examined were predominantly female. Fourteen of 32 single-school samples of 50 or more specimens were more than 60% female, whereas none was more than 60% male. The largest single-school sample examined (342) was almost half and half males and females.

Sex ratio changes with age (Table 10). This is, of course, making the assumption that the samples examined were representative of the population. Neonates and two-tone animals were almost equally divided between the sexes, but only about

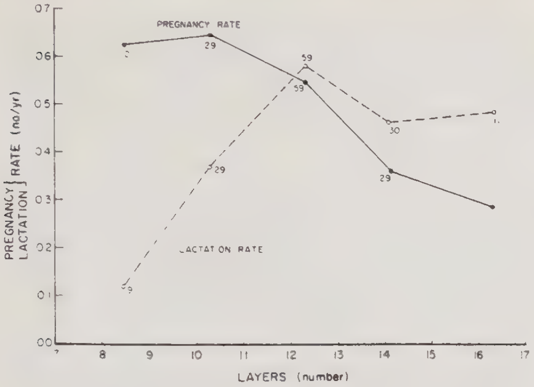

FIGURE 35.—Age-related changes in pregnancy (solid line) and lactation rates (dashed line) in *Stenella attenuata*, based on tooth layer data. Postreproductive females not included.

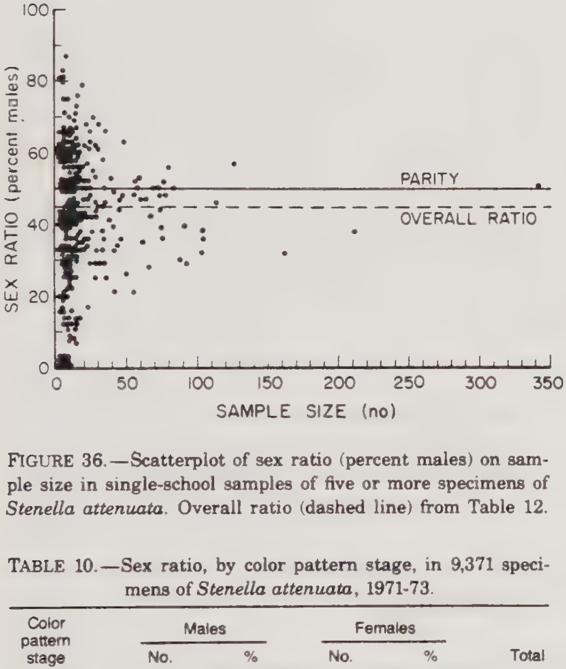

FIGURE 36.—Scatterplot of sex ratio (percent males) on sample size in single-school samples of five or more specimens of *Stenella attenuata*. Overall ratio (dashed line) from Table 12.

TABLE 10.—Sex ratio, by color pattern stage, in 9,371 specimens of *Stenella attenuata*, 1971-73.

Color pattern stage	Males		Females		
	No.	%	No.	%	Total
Neonate	205	49.8	207	50.2	412
Two-tone	666	48.7	701	51.3	1,367
Speckled	609	47.8	666	52.2	1,275
Mottled	569	43.8	729	56.2	1,298
Fused	2,154	42.9	2,865	57.1	5,019
Total	4,203	44.9	5,168	55.1	9,371

43% of the adults examined were males. The greatest change in ratio, from 48.0 to 43.5% male, comes about during the transition to mottled coloration between 7 and 8 layers of age. Assuming random sampling of the population, male and female mortality rates must diverge sharply at this point.

Gross Annual Production

An estimate of average gross annual production of calves for 1971 to 1973 was calculated based on the estimate of annual pregnancy rate, the color pattern phase data, and the proportions of mottled and fused females found to be sexually mature (Table 11).

Seven hundred and twenty-nine of 9,371 animals were mottled females (7.8%) and 2,865 were fused females (30.6%). Of 127 mottled and 1,141 fused females, 47.4 and 88.4% were sexually mature, respectively (Table 11). Average pregnancy rate was 0.469. Production = [(0.078 × 0.474) + (0.306 × 0.884)] 0.469 = 0.144 of the population per year.

TABLE 11.—Sexual maturity (presence of ovarian corpora) in mottled and fused females of *Stenella attenuata*, 1971-73.

	Mottled			Fused		
		Mature			Mature	
Year	*N*	No.	%	*N*	No.	%
1971	6	5	(—)	99	82	(82.8)
1972	92	37	(40.2)	473	417	(88.2)
1973	170	85	(50.0)	569	510	(89.6)
Total	268	127	(47.4)	1,141	1,009	(88.4)

Schooling in Relation to Reproduction

Kasuya (1972) reported changes in structure and size of schools of *S. coeruleoalba* correlated with breeding condition and breeding activities. Kasuya et al. (1974) proposed a complex hypothetical system of school formation and breakdown determined by reproductive activities in the Japanese population of *S. attenuata*. They suggested that juveniles of *S. attenuata* in Japanese waters leave breeding schools and school separately, rejoining the breeding schools at puberty. There is nothing to indicate that this happens in the eastern Pacific. We examined the coloration structure (= age structure) of single-school samples. Of 324 single-school samples of seven or more animals, only 1 (of 17 animals) contained no adults (or neonatal calves, which would indicate presence of adult lactating females in the school). This sample (8 two-tone, 2 speckled, and 7 mottled) was from a school of about 600 spotted porpoise, *S. attenuata*, congregated with about 600 spinner porpoise, *S. longirostris*. Given that about half the animals examined were adults, the probability of a single-school sample of seven containing no "fused" individuals is about 0.01 (= 0.5^7). If schools consisting only of juveniles were common, many more all-juvenile samples would have been encountered. Conversely, juveniles (two-tone, speckled, and/or mottled) occurred in all but 3 of the 324 samples. It must be concluded that juveniles probably do not school separately in the eastern Pacific. Another possibility, albeit unlikely, is that all-juvenile schools exist but are not captured by tuna seiners.

COMPARISON WITH THE JAPANESE POPULATION

Many of the estimates of life history parameters presented here differ from those published by Kasuya et al. (1974) for the relatively unexploited population of *S. attenuata* in Japanese waters (Table 12). The differences could be caused by 1) differential procedures or analytical methods, 2) intrinsic racial differences between the populations, or 3) differential population status, e.g., exploited versus unexploited. The comparisons below of similarly calculated average estimates, of course, rest on the assumption that the overall samples in both cases were not biased with respect to age or sex. The major sampling differences between the two studies is that the Japanese sample consisted mostly of large samples from a few schools, whereas our sample consisted mainly of aggregated, small samples from many schools. Both studies assume no sampling bias. Comparison of large, single-month samples in the present study with large, single-school samples in the Japanese study (e.g., the October 1972 sample in Figures 15 and 16 with sample number 2 in Figure 2 of Kasuya et al. 1974) indicate very similar length-frequency distributions and support the idea that the aggregated samples are probably not biased, or, if biased, are biased in the same way. This inference is, of course, based on the assumption that the underlying population structures are about the same in the two populations.

The estimate of Kasuya et al. (1974) of length at birth was based on only 5 full-term fetuses and newborn calves versus 86 in the present study. Our estimate can, therefore, be considered more reliable, although the possibility does exist that length at birth is greater in the Japanese population. The difference between the estimated lengths at 1 yr for the two populations is about the same as the difference between the estimates of length at birth. Estimated length at attainment of sexual maturity and maximum length (for males) are also greater for the Japanese samples. The estimate of length at maturity of males is greater in spite of the fact that Kasuya et al. used a lower testis-weight criterion than we did (68 versus 100 g). The average lengths of both adult males and

TABLE 12.—Comparison of estimates of average life history parameters of *Stenella attenuata* by Kasuya et al. (1974) and in present paper.

Parameter (average)	Kasuya et al.	Perrin et al.
1. Length at birth	89 cm	82.5 cm
2. Growth rate in 1st year	4.5 cm per mo	4.6 cm per mo
3. Length at 1 yr	143 cm	138 cm
4. Length at onset of sexual maturity:		
Males	197 cm	~195 cm
Females	187 cm	181 ± 1 cm
5. Age at onset of sexual maturity:		
Males	10.3 layers (10.3 yr)	12 layers (6-11 yr)
Females	8.2 layers (8.2 yr)	9 layers (4.5-8 yr)
6. Average length of sexually mature adults:		
Males	204-207 cm	200.7 cm
Females	192-195 cm	187.3 cm
7. Maximum length:		
Males	234 cm	226 cm
Females	220 cm	220 cm
8. Maximum number of consistently readable tooth layers	~13	12-13
9. Average ovulation rate (based on layers)	0.8 per layer (0.8 per yr)	~1 per layer (1 or 2 per yr) in fully mature, more in younger
10. Pregnancy rate (overall)	0.27 per yr	0.47 per yr
11. Breeding seasons	3 per yr	multiple
12. Gestation	11.2 mo	11.5 ± 0.2 mo
13. Lactation	29.3 mo	11.2 mo
14. Resting	9.8 mo	3.3 mo
15. Length of calving interval	4.19 yr	2.17 yr
16. Sex ratio:		
Overall	0.76 male:1 female	0.81 male:1 female
At birth	1.3-1.5:1	1.00:1
Adults	0.58:1	0.75:1

females are also greater in the Japanese population, and in this case, all four of the estimates are based on large and certainly adequate samples. These differences all suggest that the Japanese form is about 6 to 8 cm larger than the eastern Pacific form.

The estimates of Kasuya et al. (1974) of age at attainment of sexual maturity are based on their conclusion that one tooth layer corresponds to 1 yr of growth. It appears from comparisons of their first-year growth curve with ours (note rate in first year and length at 1 yr) that our first two layers correspond to their first layer. Kasuya (1972) in his paper on growth of *S. coeruleoalba* mentioned observing "one or two faint translucent layers in the thick opaque layer accumulated just after the birth" that were "not used for age determination because it was not expected to show the annual accumulation cycle," and Kasuya et al. (1974) stated that the "dentinal growth layers of this species [*S. attenuata*] does not differ so much from that of *S. coeruleoalba*." After the first year, our hypothesis 2 corresponds to the assumption of Kasuya et al. of one layer per year, e.g., nine layers of Perrin et al. (1973) = eight layers of Kasuya et al. = 8 yr.

The average length of calving interval in both studies was estimated by several methods that converged on the respective central estimates. One minor difference between the two analyses is that Kasuya et al. (1974) did not exclude postreproductive females from the "resting/estrus" group. Thus, their estimate of the average resting/estrus period of 9.8 mo may be a slight overestimate. The probable effect of this on the estimate of length of total calving interval is very small, however, and it therefore seems that the estimates are analytically comparable and that the difference between them is real. Kasuya et al. estimated that individual intervals in the Japanese population vary from 23 to 60 mo, with modes at 28 to 30, 36 to 38, and 54 to 56 mo. The potential thus probably exists for a shift in average length from 50 mo (4.17 yr) to 26 mo (2.17 yr) under exploitation.

Kasuya et al. (1974) used the same methods used here to estimate length of the lactation period and arrived at a "best" estimate of 29.3 mo, some 18 mo longer than our estimate of 11.2 mo. They found that the major shift from milk to solid food occurs at body length of about 133 cm, about the same as in our sample, but that some suckling and lactation of the mother continues for an average additional 20 mo. The prolonged suckling is probably nutritionally a largely nonfunctional aspect of general prolonged parental care. It has been suggested on the basis of comparison of the life histories and behavior of mysticetes and odontocetes that this period in odontocetes may allow for "sophisticated" communicational-navigational training (Brodie 1969). Thus the apparent shorter lactation period in the eastern Pacific, and the concomitant shorter calving interval and higher pregnancy rate, does not necessarily mean earlier effective weaning, but may reflect a truncated parental care period.

The apparent overall sex ratios are almost the same for the two populations, but the proportion of males was higher at birth and lower at maturity in the Japanese samples than in the eastern Pacific samples. A lower proportion of males at birth could be a response to exploitation. Kasuya et al. (1974) suggested that the very low proportions of males in mature age-classes in the Japanese catches could be partially caused by segregation of adult males or by differential catchability but are largely due to differential mortality rates. If the decrease in proportion of males with age is caused by differential mortality, the apparent faster decrease in the Japanese population must mean that the disparity in mortality rates between the sexes is greater there than in the eastern Pacific.

In summary, the two sets of estimates differ in a consistent way, and the differences are real. It seems possible that the differences in some way reflect exploitation in the eastern Pacific.

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SHORT PAPER

DESCRIPTION OF THE MALE OF THE HAWAIIAN ANGELFISH *GENICANTHUS PERSONATUS*

John E. Randall and Paul Struhsaker

ABSTRACT

Only four female specimens were available for the description of the Hawaiian angelfish *Genicanthus personatus* by Randall (1975). Since the eight other species of the genus are all sexually dichromatic, the existence of a male of different color was predicted. Two male specimens of this species were recently trawled at a depth of 51 m near Nihoa Island in the Leeward Hawaiian Islands. They were light gray with a broad black band across the base of the caudal fin like the females, but in sharp contrast to the females, the front of the head and most of the pectoral, dorsal, and anal fins were yellow-orange. Also, the males were more elongate, the depth 2.1 in SL, and the caudal fin was lunate instead of emarginate due to a prolongation of the lobes of the fin.

The first pomacanthid fish of the genus *Genicanthus* from the Hawaiian Islands, *G. personatus*, was described recently (Randall, 1975) from four female specimens taken in the depth range of 23-84 m. The lack of a male specimen was unfortunate, because it was anticipated the male would be different. Randall wrote, "In view of the marked sexual dichromatism of all the other species of the genus, it seems likely that the male of *G. personatus* will also have a different color pattern." He added, "Of the known species of *Genicanthus*, this species most resembles the '*fucosus*' form of *G. semifasciatus*. If there is a different male color phase of *G. personatus*, it might be expected to have numerous poorly defined bars on the upper part of the body."

The first two specimens of *personatus* to be catalogued after the description were also females. One of 72 mm SL was collected in 28 m of water off Oahu between Waianae and Campbell Industrial Park by Fern Kealoha in 1973. It was maintained in an aquarium for an unspecified period. Upon the death of the fish, it was presented to the Bishop Museum by Glenn Takeshita. It is now catalogued under BPBM 19208. The second fish (BPBM 19647, 107 mm SL) was collected at 20 m in a cave at Moku Manu, Oahu by John Earle and Dan Johnson in September 1975. It was 52 m from the entrance to the cave (the divers were using a light). The fish was placed in an aquarium but would not take food. It survived without feeding for 2 months.

On 26 October 1975 two males of *G. personatus* (BPBM 19648, 153 and 155 mm SL) were captured during cruise 67 at station 15 of NOAA research vessel Townsend Cromwell in the Leeward Hawaiian Islands. The capture locality was 23°08′N, 161°53′W over the insular shelf north of Nihoa Island at a depth of 51 m. The bottom temperature as indicated by XBT drops was 25°-26°C. The specimens were taken during a 20-minute haul (median time 2053 h) with a high-opening bottom fish trawl with a 20.1-m headrope and a 25.3-m footrope constructed of 100-mm mesh webbing in the body and cod end.

The first prediction, that the male would be different, proved to be true; the second, that it would have bars on the body, did not.

Description.—Dorsal rays XIV,17; anal rays III,17; pectoral rays 17; scale rows from upper end of gill opening to caudal base 47-48; gill rakers 4 + 12; serrae on upper margin of preopercle 34-36.

Depth of body 2.12-2.13 in SL; width of body 2.76-2.77 in depth; head length 3.65-3.69 in SL; snout length 2.89-2.93 in head; diameter of eye 3.36-3.44 in head; bony interorbital width 2.76-2.89 in head; length of preopercular spine 2.24-2.27 in head; least depth of caudal peduncle 2.01-2.03 in head; caudal fin lunate, the caudal concavity 3.48-3.83 in SL; length of pectoral fin 1.25-1.28 in head; last dorsal spine 1.51-1.54 in

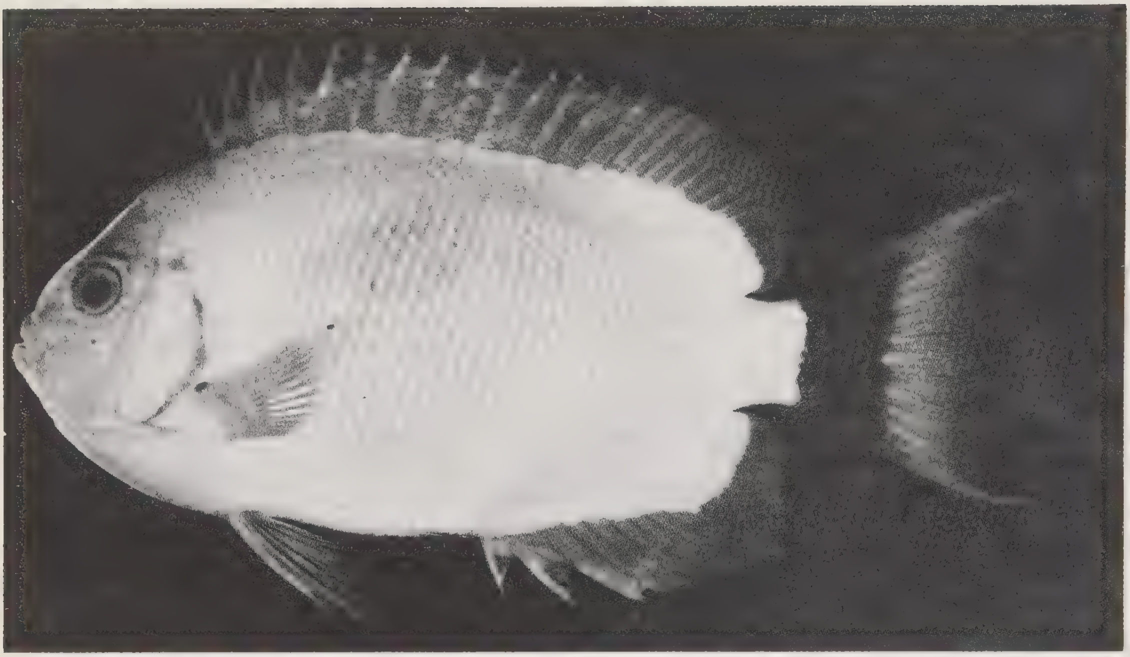

Figure 1. The 155-mm SL male *Genicanthus personatus* (BPBM 19648).

head; longest dorsal soft ray 5.20-5.38 in SL; third anal spine 1.25-1.29 in head.

Coloration of the fresh 155-mm SL specimen is shown in Figure 1. Color in alcohol: body light gray, the edges of the scales brownish gray except posterior third of caudal peduncle which is black (merging with black at base of caudal fin); head brownish gray posteriorly, abruptly pale (nearly white) anterior to upper margin of preopercle and a wavy line of demarcation extending dorsally from upper end of margin nearly to mid-dorsal line, thence to origin of dorsal fin (thus leaving a narrow median pale band on nape running anterior to fin); isthmus and ventral part of thorax pale nearly to pelvic fins; opercular membrane pale; dorsal and anal fins pale except for a basal zone of grayish brown which in the dorsal begins at base of 12th dorsal spine (and for the anal the base of the first anal ray) and broadens to half the height of these fins on about posterior half of the soft portions; caudal fin black on nearly the basal half, some blackish extending out onto lobes, gray on rest of fin; paired fins pale. All the pale areas on the preserved specimens are yellow-orange in life (except outer fourth of pectoral fins which is clear), the remainder light gray except for the broad black bar on caudal peduncle and base of caudal fin and some light orangish color on the caudal lobes.

Remarks.—The males of *G. personatus* share the light gray color of the body and posterior head of the females, the broad black band across the base of the caudal fin and adjacent caudal peduncle, and yellow-orange pelvic fins. They differ in the yellow-orange anteriorly on the head and over much of the dorsal, anal, and pectoral fins. The yellow-orange coloration of the pelvic fins extends to the fin insertions of the males. There are also some important morphometric differences. The body of the males is more elongate (about 2.1 in SL compared to 1.8) and the caudal fin lunate (primarily as a result of prolongation of the upper two and lower

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two branched rays) instead of emarginate. Also the preopercular spine of the males is longer, the snout shorter, and the dorsal and anal fins shorter.

The total fish catch of the haul resulting in the two specimens of *G. personatus* was 32 kg. Twenty-two other species of fishes were taken, of which the dominant ones (by weight) were *Mulloidichthys vanicolensis* (*auriflamma* of most recent authors), *Acanthurus olivaceus*, *Naso lopezi*, *Flammeo scythrops*, *Chaetodon miliaris*, *Priacanthus alalaua*, and *Heniochus acuminatus*.

The northwestern portion of the Hawaiian Archipelago comprises numerous peneplained banks with mean depths ranging from about 25 to 65 m. Limited evidence suggests that these smooth bank tops are almost entirely devoid of sediments and have sparse numbers of the corals *Porites lobata* and *Pocillopora eydouxi*. Two small samples of algae taken from the trawl at stations in 51 m near Nihoa Island and 29-37 m near Gardner Pinnacles yielded the following readily identifiable forms: *Amansia glomerata*, *Ceramium* sp., *Champia* sp., *Chondria* sp., *Codium reediae*, *C. saccatum*, *Dictyopteris repens*, *Dictyosphaeria cavernosa*, *Halimeda gracilis*, *H. discoidea*, *Herposiphonia* sp., and *Microdictyon secthellianum*. In these and other hauls in the general area of collection, the dominant (by weight) algae in the trawl catches were *Codium*, *Halimeda*, and *Amansia*.

The stomach of one of our two specimens of *G. personatus* was empty; the other was filled with the green alga *Codium* sp.; in addition there were a few shrimp larvae and fish eggs.

G. personatus was named for the black masklike area on the anterior upper part of the head of the female, which encloses the eye. The male has replaced the black with a yellow-orange mask. The common name "Masked Angelfish" is proposed for this species.

ACKNOWLEDGMENTS

We are grateful to Drs. Mitchell D. Hoyle for the algae determinations and James E. Maragos for identification of the corals.

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Length Composition of Yellowfin, Skipjack, and Bigeye Tunas Caught in the Eastern Tropical Atlantic by American Purse Seiners

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ABSTRACT

Sampling and analytical procedures that are used to estimate the size composition of Atlantic tunas caught by American purse seiners in the eastern tropical Atlantic are described. The procedures are based on a stratified, two-stage subsampling model. Estimates indicated that about 0.2 to 1.4 million yellowfin tuna, *Thunnus albacares*, 1.2 to 12.8 million skipjack tuna, *Katsuwonus pelamis*, and 0.5 to 41.2 thousand bigeye tuna, *T. obesus* were caught annually by the fleet in 1968-74. The dominant age group in most years was 1-yr olds for yellowfin and skipjack tuna and 2-yr olds for bigeye tuna.

INTRODUCTION

United States participation in the eastern tropical Atlantic tuna fishery off west Africa began in the 1950's. It was not until 1967, however, that significant numbers of U.S. purse seiners entered the fishery (Sakagawa and Lenarz 1972; Sakagawa 1974). Since then as many as 36 American[3] seiners have participated annually in the fishery.

The American tuna fleet that fishes in the eastern Atlantic consists primarily of purse seiners of 80 to 1,800 metric tons carrying capacity of fish. Home bases for U.S. vessels are in California and Puerto Rico; the eastern Atlantic is only one of several areas where the vessels fish in a year. Each seiner has upwards of 20 fish-holding wells that freeze and store an average of about 60 metric tons of tuna per well.

The fishing season in the eastern tropical Atlantic, while year round for most fleets, begins about July and usually ends in November-December for most American vessels. The American vessels generally fish in close proximity to each other, although they are operated by independent captains. Their catch consists of yellowfin, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*, tunas primarily and some bigeye tuna, *T. obesus*, and incidental catches of little tunny, *Euthynnus alletteratus*, frigate and bullet mackerels, *Auxis* spp., and rainbow runner, *Elagatis bipinnulata*. In 1967-69, more than half the catch was yellowfin tuna; since 1969, skipjack tuna has been the dominant species in the catch (Sakagawa and Lenarz 1972). Virtually all the U.S. catch is returned to the United States aboard the seiners or aboard transshipment vessels for processing, canning, and marketing. Transshipments were made in 1970-74.

Monitoring of the American catch to assess stock abundance was initiated by the National Marine Fisheries Service (NMFS), NOAA, in 1968 and continued annually since then. Catch, effort, and length-frequency samples are collected by NMFS representatives and under contract by the Inter-American Tropical Tuna Commission (IATTC) representatives. Summaries of catch and effort data were reported in Sakagawa and Lenarz (1972) and Sakagawa (1974). This report presents a description of procedures used to estimate the length composition of tunas in the American catch and the estimated length composition of tunas caught in 1968-74.

SAMPLING PROCEDURES

Tuna catches were sampled for length-frequencies aboard the seiners during unloadings at canneries in California and Puerto Rico in 1968-74, and during unloadings at freezer storage facilities and onto transshipment vessels in west Africa in 1971-73. Samples were also obtained from transshipment vessels that unloaded at canneries in California and Puerto Rico.

Sampling in west Africa was particularly critical in 1971 because in that year, and in 1970 to a lesser degree, large yellowfin and bigeye tunas with presumably high mercury content were selectively shipped to Europe, where a higher mercury content was acceptable, rather than to the United States. Samples taken only in California and Puerto Rico in those years were therefore biased.

Sampling in west Africa also presented the opportunity of sampling the transshipped catch before it was mixed in the holds of the transshipment vessels. Upwards of 700 metric tons of fish have been transported in a hold of a transshipment vessel. The transshipped catches of individual seiners are kept separate, but an entire seiner's catch, which is usually caught in several areas and over several months, is generally loaded into a single hold.

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[3] The fishing operations of Canadian, Dutch (based in Willemstad, Netherlands Antilles), Panamanian, and U.S. boats fishing in the eastern tropical Atlantic are monitored as a unit by the Inter-American Tropical Tuna Commission. "American" in this report refers to this fleet, which in 1968-73 consisted of at least 83% U.S. seiners.

Length-Frequency Samples

The sampling procedures were virtually the same as those recommended by Hennemuth (1957) for the eastern tropical Pacific fishery, i.e., a stratified, by area and month, two-stage subsampling procedure (Cochran 1963) was used. The boundaries of the areas (Fig. 1) were drawn according to the distribution and concentration of fishing effort of the American fleet.

The first stage of the sampling was to choose the well (or hold if a transshipment vessel[4]) to sample. The second stage was to draw from the selected well a random sample of each species (yellowfin, skipjack, and bigeye tunas). Ancillary information, such as well number and catcher vessel name, was recorded for each sample. The date, location (NMFS area — Fig. 1), and tonnage of the catch sampled were obtained from logbooks after the samples were drawn.

Before 1972, samples were obtained on an opportunistic basis and the sample size varied (10 to 300 fish). Since 1971, a goal of 6 skipjack samples and 12 yellowfin samples of 50 fish each from each NMFS area and each fishing month was established in an attempt to ensure a more complete area-month coverage. The larger number of samples for yellowfin tuna was required because of the greater variability in sizes of this species (Hennemuth 1957). This goal, however, was not attained in any of the years.

Total Catch by NMFS Area-Month

Total catch, by species and month, of tunas caught in the Atlantic by American vessels is tabulated annually by the IATTC from landing receipts. Logbook information on estimated catch by species, 1° area, date, and well number in which the catch is stored for each net set is also collected by the IATTC from virtually the entire American fleet. This logbook information was used to identify those seine sets that contributed to the catch in wells that were sampled and also to prorate the total catch by species of the entire fleet into catch by NMFS area-month strata.

ANALYTICAL PROCEDURES

Different areas apparently contain different sizes of fish, at least for yellowfin tuna in the eastern tropical Atlantic (International Commission for the Conservation of Atlantic Tunas 1974a), and the stratified sampling procedure, by month and area, was designed to account partly for this difference. Sizes of fish in the total American catch were estimated from the stratified length-frequency samples and catch.

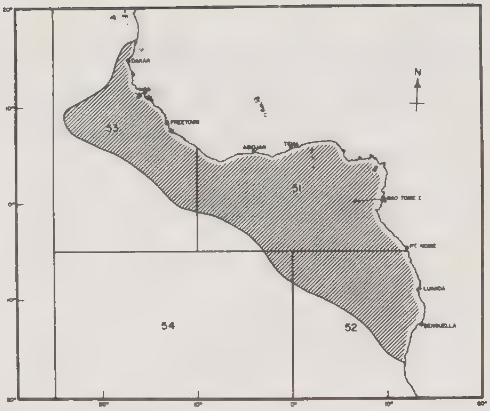

Figure 1.—Map of the eastern tropical Atlantic where American seiners fish for tropical tunas (shaded area). Numbered statistical areas used in this report are shown.

When a sample is drawn from a well, complete information on date, location, and tonnage of catch is not always available; complete information is obtained later from the ship's logbook. Fish that may have been caught in different strata were, consequently, sometimes drawn in a single sample. These samples were not used in our analysis unless 75% or more of the tonnage in the well was caught in a single NMFS area-month stratum. Because of this rule, virtually all samples from transshipment vessels were not used in this study. Analyses currently underway which contain a special stratum for transshipment samples may lead to new procedures for utilizing much of the rejected samples.

Weighting Factor

The sample size was fixed and not proportional to the numbers of fish in the well. Each sample was therefore weighted by a factor (number of fish) based on the species tonnage and average weight of fish in the well or, when this was unavailable, on the species tonnage and average weight of fish in seine sets that contributed to the catch in the sampled well.

Substituting Samples

Samples were unavailable for all area-month strata in which the fleet caught fish. For strata without samples, it was necessary to make assumptions about the catch and substitute samples from adjacent strata, within year to estimate the sizes of fish caught by the fleet. Substitution was on the basis of the following rules: 1) use same month and adjacent areas; 2) use same area and adjacent months; 3) use adjacent months and adjacent areas. These rules are ordered according to priority and are based on the assumption that differences in sizes of fish from widely separated areas or months are greater than differences in sizes of fish from adjacent areas or months.

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[4] It is not uncommon to find several species stored in a well. The fish are partially thawed in the wells before unloading at the canneries or onto a transshipment vessel. Measurements were made on partially thawed fish.

In Tables 1 and 2 the area-month strata with substituted samples are shown for yellowfin and skipjack tunas caught in 1968-74. About 20 to 60% of the strata in which yellowfin tuna were caught and about 10 to 60% of the strata in which skipjack tuna were caught had no samples and substitutes were necessary (Table 3). In terms of tonnage, substitutions were required for 2 to 29% of the total yellowfin tuna catch and 1 to 17% of the total skipjack tuna catch.

The poorest sampling coverage of yellowfin and skipjack tunas was in 1970. In that year, representative sampling was difficult because large yellowfin and bigeye tunas were transshipped in west Africa to foreign ports and not sampled. The best sampling coverage, in terms of tonnage, was in 1969 for yellowfin and 1971 for skipjack tuna.

Estimating Length Composition of Catch

Length-frequency of fish in the total catch by species was computed by summing estimates for each area-month stratum. The following procedures were used for the stratum estimates:

1. The weight (w in kilograms) of each fish was estimated from length (l in centimeters) based on the appropriate length-weight equation (Lenarz 1974) shown below. The average weight ($\bar{w}_i$) of fish in the sample, $i = 1, 2, \ldots, k$, was then estimated.

Table 1.—Catch (metric tons) and number of length-frequency samples of yellowfin tuna by NMFS area-month strata. Samples substituted in strata without samples are identified in parentheses.

Month - year		Area 53		Area 51		Area 52	
		Catch (tons)	Samples	Catch (tons)	Samples	Catch (tons)	Samples
January	1974			88	(July-51)	9	(July-51)
February	1974			11	(July-51)		
March	1974			33	(July-51)	2	(July-51)
May	1970			4	(June-51)		
	1972			363	1	11	(May-51)
June	1970			682	6	3	(June-51)
	1972	21	(June-51)	613	2		
	1974			95	(July-51)		
July	1969			605	1		
	1970			1578	5		
	1971			471	2		
	1972	34	(July-51)	1676	5	51	(July-51)
	1973			670	3		
	1974			1292	5		
August	1968			1995	7		
	1969			6786	8		
	1970			3207	3		
	1971	8	(Aug-51)	1730	10		
	1972	8	(Aug-51)	3955	14	993	3
	1973			369	(Aug-52)	867	3
	1974			1405	7	95	(Aug-51)
September	1968			1384	3	1352	3
	1969			5195	10	2	(Sept-51)
	1970	494	1	1769	(Sept-53)		
	1971			353	1	920	6
	1972	20	(Oct-53)	124	(Sept-52)	1059	5
	1973			9	(Sept-52)	261	3
	1974					51	(Oct-52)
October	1968			143	1	953	(Oct-51)
	1969			3643	4	351	(Oct-51)
	1970	962	3	12	(Oct-53)	597	(Oct-53)
	1971	8	1	93	2	179	1
	1972	1665	4	943	4	176	(Oct-51)
	1973			405	2	7	(Oct-51)
	1974			647	2	836	2
November	1969			3178	4	1	(Nov.-51)
	1970	36	(Oct.-53)	69	(Oct.-53)	398	(Oct.-53)
	1971	41	(Oct.-53)	31	(Oct.-51)		
	1972	344	[illegible]	28	1	18	(Nov.-51)
	1973			706	1		
	1974	28	(Nov.-51)	429	3	355	3
December	1974			191	1	53	(Dec.-51)

Table 2.—Catch (metric tons) and number of length-frequency samples of skipjack tuna by NMFS area-month strata. Samples substituted in strata without samples are identified in parentheses.

Month - year	Area 53		Area 51		Area 52	
	Catch (tons)	Samples	Catch (tons)	Samples	Catch (tons)	Samples
January 1974					133	(July-51)
February 1974			10	(July-51)		
March 1974			48	(July-51)	24	(July-51)
May 1970			29	(June-51)		
1972			334	2		
June 1970			1007	5	11	(June-51)
1972	130	(June-51)	703	3		
1974	5	(July-51)	171	(July-51)		
July 1969			161	1		
1970			1375	6		
1971			423	2		
1972	419	2	1504	4	121	(July-51)
1973			214	(Aug-52)		
1974			1245	5		
August 1968			1206	2		
1969			2443	14		
1970			4441	3		
1971			1119	9		
1972	75	2	1465	9	1811	6
1973			94	(Aug-52)	6175	22
1974			899	6	443	1
September 1968			1049	3	265	2
1969			1011	9	1	(Sept-51)
1970	428	(Sept-51)	1935	2		
1971			402	1	6549	19
1972	5	(Sept-51)	701	2	2124	7
1973			19	(Sept-52)	11465	28
1974					10796	10
October 1968			268	1	375	1
1969			1071	5	155	(Oct-51)
1970	1087	3	4	(Oct-53)	814	(Sept-51)
1971	46	(Oct-51)	3155	6	3725	9
1972	826	7	1180	7	379	2
1973			56	(Oct-52)	4189	13
1974			308	1	2453	6
November 1968					15	(Oct-52)
1969			43	1	7	(Nov-51)
1970			23	(Oct-53)	643	(Oct-53)
1971	218	1	1191	1		
1972	382	5	34	(Nov-53)	9	(Oct-52)
1973			82	2		
1974	45	(Nov-51)	275	1	810	1
December 1974			102	(Dec-52)	2207	8

yellowfin tuna

$w = (2.18 \times 10^{-5})\, l^{2.970}$

skipjack tuna

$w = (5.61 \times 10^{-6})\, l^{3.315}$

bigeye tuna

$w = (1.25 \times 10^{-5})\, l^{3.121}$

2. Average weight was used to convert the well tonnage (S_i) from which the *i*th sample was taken to numbers of fish ($M_i = S/\bar{w}_i$).
3. M is distributed proportionately by 2-cm intervals, according to the length-frequency distribution of the *i*th sample.
4. A weighted average weight ($\bar{\bar{w}}$) of fish in all the samples of a stratum was estimated with M_i as the weighting factor, $\bar{\bar{w}} = \Sigma(M_i \bar{w}_i)/\Sigma M_i$.
5. The number of fish (N) in the total catch (C) of a stratum was estimated with $N = C/w$.
6. The length-frequency distributions of all M_i's of a stratum were pooled and the pooled frequency distribution was used to estimate the length composition of N.

Table 3.—Sampling coverage of NMFS area-month strata in which yellowfin and skipjack tunas were caught by American tuna seiners in 1968-74.

Species-year	Area-month strata[1]			Catch			Samples	
	Total (number)	Sampled		Total (tons)	Sampled		Total (number)	Number/ Catch of 1,000 tons
		Number	Percent		Tons	Percent		
Yellowfin								
1968	5	4	80.0	5,830	4870	93.8	14	2.40
1969	8	5	62.5	19,760	19,410	98.2	27	1.37
1970	13	5	38.5	9,810	6,920	70.6	18	1.83
1971	10	7	70.0	3,830	3,750	97.9	51	13.31
1972	19	10	52.6	12,100	11,640	96.2	43	3.55
1973	8	5	62.5	3,300	2,910	88.3	12	3.64
1974	17	7	41.2	5,620	5,160	91.7	28	5.00
Skipjack								
1968	6	5	83.3	3,180	3,160	99.5	9	2.83
1969	8	5	62.5	4,890	4,730	96.7	31	6.34
1970	12	5	41.7	11,790	9,840	83.5	19	1.61
1971	9	8	88.9	16,830	16,780	99.7	59	3.51
1972	18	13	72.2	12,200	11,900	97.6	58	4.75
1973	8	4	50.0	22,290	21,910	98.3	67	3.01
1974	17	9	52.9	19,970	19,440	97.3	39	1.95

[1] Only strata in which a catch was made are included.

ESTIMATES OF LENGTH COMPOSITION OF CATCHES

Yellowfin Tuna

The estimated length compositions of yellowfin tuna in the 1968-74 catches by month strata, all areas combined, are shown in Appendix Tables 1 to 7. Area differences are presumed to be not as significant as monthly differences within a year.

As many as four modal groups are found in the length-frequency distributions, but only two or three are prominent (Fig. 2). The prominent modes correspond to the apparent entering year class (approximately 33 to 47 cm long), 1-yr-old (48 to 85 cm long), and 2-yr-old (86 to 123 cm long) fish. The modal size of the apparent entering year class is peculiar in that it differs from the modal size of the 1-yr-old fish by about 18 cm. According to the growth curve for Atlantic yellowfin tuna of Le Guen and Sakagawa (1973), the difference should be about 57 cm if the two groups are 1 yr apart. Some possible causes for this difference are: 1) there is extreme sampling bias of the entering year class, and perhaps even of 1-yr-old fish in the catch, owing to differential availability or vulnerability; 2) the entering year class in fact represents slower growing or later hatching fish of the same year class as the 1-yr-old fish, i.e., from multiple spawnings (Richards 1969); or 3) that the growth curve of Le Guen and Sakagawa (1973) is incorrect. Both 1) and 2) are probably the major causes for the difference. Hennemuth (1961) similarly identified length modes that were less than a year apart in age and presumably from identical year classes or subpopulations of yellowfin tuna from the eastern tropical Pacific.

In 1968-74, about 0.2 to 1.1 million yellowfin tuna were caught annually by the American fleet in the eastern tropical Atlantic. The age-frequency distributions of the catches (Table 4), based on analysis of modal progression and the growth curve of Le Guen and Sakagawa (1973), indicate that the dominant age group was 1-yr-old fish in 1968 and 1970-74, and 2-yr-old fish in 1969.

The catch of 1969 is unusual compared to that of the other years. Besides the dominance of 2-yr olds in the catch of that year, the 1969 catch (in weight) of yellowfin tuna was the highest recorded for the American fleet and virtually all (98%) was taken in NMFS area 51. About 90% of the catch, furthermore, was from pure yellowfin schools, the remainder from mixed yellowfin-skipjack schools. In the other years, a smaller percentage (61 to 75%) of yellowfin tuna was caught in area 51 and only about 60% of the catch was from pure yellowfin schools. Yellowfin tuna in mixed yellowfin-skipjack schools are generally smaller than in pure yellowfin schools

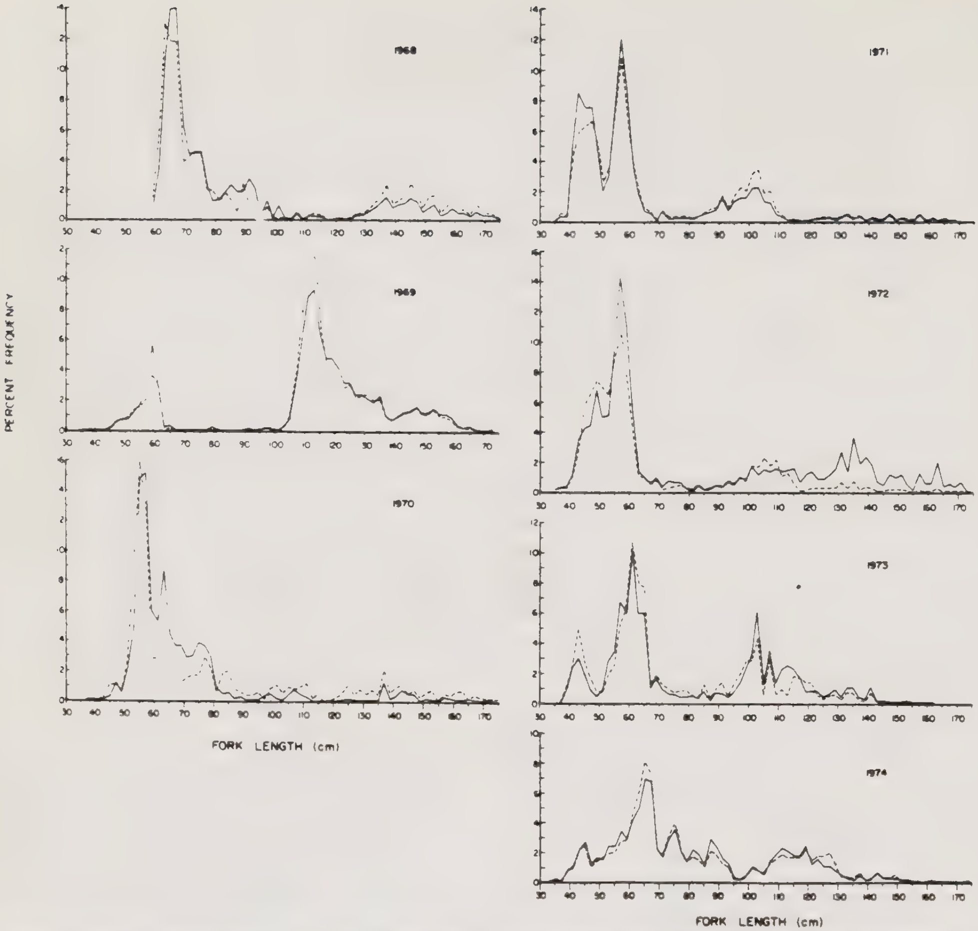

Figure 2.—Estimated length composition of yellowfin tuna caught by American seiners in the eastern tropical Atlantic, 1968-74. (Solid line — stratified procedure; dashed line — unstratified procedure.)

(Calkins 1965). The predominance of large yellowfin tuna (>100 cm) in the 1969 catch could have been caused therefore by the high percentage of pure schools fished in that year.

Skipjack Tuna

The catch of skipjack tuna by the American fleet markedly increased from 3,180 metric tons in 1968 to 22,290 metric tons in 1973, then decreased to 19,970 metric tons in 1974 (Table 3). This represents for skipjack tuna an estimated 1.2 million in 1968, 12.8 million in 1973, and 10.6 million in 1974. The estimated length composition of the 1968-74 catches by month strata, all areas combined, are shown in Appendix Tables 8 to 16.

Two apparent age groups, probably 1-yr-old (31 to 55 cm long) and 2-yr-old (56 to 67 cm long) fish, contributed to the catch (Fig. 3). The dominant group was 1-yr-old fish in all years except 1969 (Table 5).

The dominant modal length in the skipjack catch decreased from about 50 to 55 cm in 1968-70 to about 45 cm in 1971-74 (Fig. 3). This decrease, while relatively small, occurred with the discovery by the American fleet in 1971 that skipjack fishing is good off Angola (NMFS area 52) during the fall months. Before 1971 most of the

Table 4.—Estimated age composition of yellowfin tuna caught by the American purse seine fleet in the eastern tropical Atlantic.

Age group	Approximate length (cm)	Estimated catch (numbers) by year						
		1968	1969	1970	1971	1972	1973	1974
0	35-51			29,900	169,100	368,300	25,200	46,700
I	52-91	230,300	116,900	907,500	186,600	763,600	122,000	157,800
II	92-125	54,200	339,600	63,000	81,100	218,500	82,700	99,500
III	126-149	16,400	142,900	77,700	16,300	46,600	15,300	99,800
IV	150-169	38,600	41,100	25,700	7,000	15,300	700	13,400
V+	170+	19,400	3,200	7,000		2,300		
Total		358,900	643,700	1,110,800	460,100	1,414,600	245,900	417,200

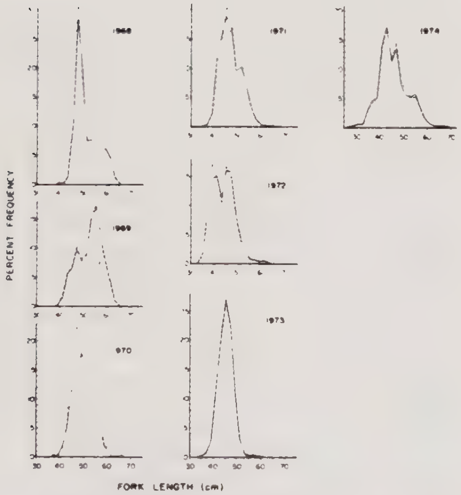

Figure 3.—Estimated length composition of skipjack tuna caught by American seiners in the eastern tropical Atlantic, 1968-74. (Solid line — stratified procedure; dashed line — unstratified procedure.)

American catch was made in the Gulf of Guinea and only about 3 to 21% of the skipjack tuna was caught in area 52. Since the discovery in 1971, as much as 98% of the annual American catch of skipjack has been taken from area 52.

Bigeye Tuna

Bigeye tuna are not often available to the surface fisheries (purse seine and pole-and-line) of the eastern tropical Atlantic. This species is sometimes confused with yellowfin tuna and catches may have been included with yellowfin tuna catches, but the amount is probably small. The American fleet reported bigeye tuna catches only in 1968 and 1971-74. A few length-frequency samples were collected in those years (Table 6). Because the samples were few, estimates of the length composition of the catch were based on all samples combined without stratification, i.e., all catches and samples pooled and one estimate calculated for each year (Appendix Table 17).

About four major modal groups (39 to 51 cm, 52 to 73 cm, 74 to 105 cm, and 106 to 131 cm) can be identified in the length-frequency distributions (Fig. 4). These groups apparently represent age groups of 1 to 4 yr, based on

Table 5.—Estimated age composition of skipjack tuna caught by the American purse seine fleet in the eastern tropical Atlantic.

Age group	Approximate length (cm)	Estimated catch (numbers) by year						
		1968	1969	1970	1971	1972	1973	1974
I	31-55	802,800	531,000	4,268,700	6,413,700	7,290,200	12,754,800	9,327,500
II	56-67	409,700	1,137,300	486,000	2,069,200	121,600	43,300	1,222,800
Total		1,212,500	1,668,300	4,754,700	8,482,900	7,411,800	12,798,100	10,550,300

Table 6.—Catch and number of length-frequency samples of bigeye tuna caught by the American purse seine fleet in the eastern tropical Atlantic.

Year	Number of samples	Catch	
		Tons	Estimated Numbers
1968	2	15	500
1971	7	540	19,700
1972	3	210	29,400
1973	3	110	10,600
1974	8	860	41,200

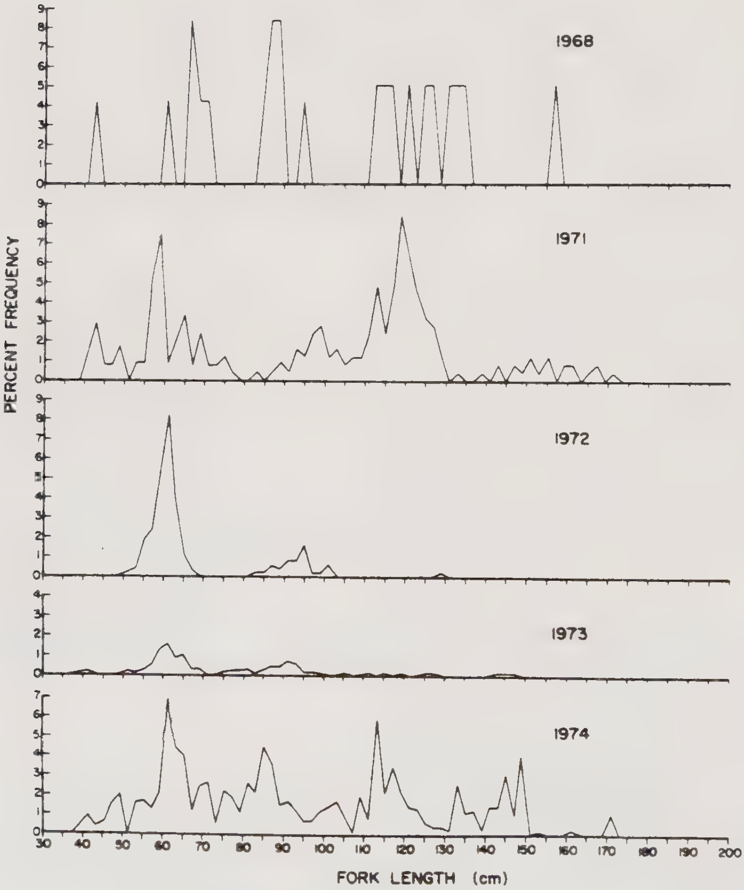

Figure 4.—Estimated length composition of bigeye tuna caught by American seiners in the eastern tropical Atlantic, 1968 and 1971-74.

Champagnat and Pianet's[6] growth curve for Atlantic bigeye tuna.

The estimated total number of bigeye tuna caught by the American fleet in 1968 and 1970-74 ranges from about 500 to 41,200 fish. The largest catch was in 1974, the smallest in 1968.

SOURCES OF BIAS IN THE ESTIMATES

Several possible sources of bias in the sampling, weighting, and substitution procedures could have significantly influenced the estimated length-frequency distributions of the catches. Some of the sources are discussed below.

Sampling Bias

Hennemuth (1957) found a slight size-depth stratification of skipjack tuna but none for yellowfin tuna in wells he examined. He mentioned that stratification could result from settling of large fish to the bottom of the well or from different schools of fish of different sizes packed in a layer fashion.

Early in our sampling program, size-depth stratification was recognized as a possible source of error and steps were taken to reduce the influence of this error by limiting sampling to wells that did not appear to contain fish that were stratified by size and depth. How effective this measure was is not known.

A more serious sampling bias was introduced in 1970 with the discovery that tunas, particularly large specimens, contain high levels of mercury which the Food and Drug Administration of the United States deemed unacceptable for U.S. markets. Canneries in the United States, therefore, limited their purchases of large fish, and American fishermen were forced either to not land large tunas or to sell the large tunas to foreign markets where the acceptable level of mercury contamination was higher. Because large yellowfin and bigeye tunas caught off Africa in 1970 and 1971 were selectively sold and transshipped from west African ports directly to foreign buyers, fish landed in the United States were biased towards the smaller fish. This bias probably affected our estimates for 1970. Estimates for 1971 were not affected because catches transshipped to foreign ports were sampled in west African ports prior to transshipment.

Weighting Bias

Some of our length-frequency samples were weighted by a factor (number of fish) based on the total tonnage and average weight of fish in sets that contributed to the catch in the sampled well. As indicated earlier, this technique was used because the sample size was not proportional to the numbers of fish present and the amount of tonnage in the well was not known. The use of the total tonnage, instead of the tonnage in the sampled well only, to base a weighting factor introduced a bias of overweighting the samples. For example, a sample from a well containing 20 tons of fish from a 80-ton set A and 40 tons from a 40-ton set B would have a weighting factor based on 120 tons, causing the sample to be disproportionately weighted by the catch of set A.

We examined this bias with the August 1973 yellowfin tuna catch of area 52 (Table 1) in which the actual tonnages of fish in the three sampled wells were available. A biased estimate length composition of the catch was derived with weighting factors based on tonnages of 127, 41, and 17 for the three samples. An unbiased estimated length composition of the catch was derived with weighting factors based on the actual tonnages in the sampled wells of 60, 20, and 15, respectively. The unbiased and biased estimated length compositions of the catch are not very different (Fig. 5). However, the total estimated number of yellowfin tuna is 7% higher in the unbiased than in the biased estimate, owing to the greater numbers of small fish (<61 cm) in the unbiased estimate.

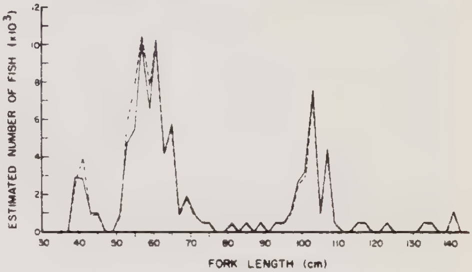

Figure 5.—Estimated length composition of yellowfin tuna caught in August 1973 in NMFS area 52. (Solid line — biased weighting factors; dashed line — unbiased weighting factors.)

Substitution Bias

Of all the possible sources of bias in our estimates, substitution bias perhaps is the most serious. As indicated earlier, 11 to 61% of the strata were not sampled and required substitution of samples from adjacent strata. Furthermore, not all of the sampled strata were sampled adequately. Between 20 to 43% of the strata sampled for yellowfin tuna and 0 to 33% of the strata sampled for skipjack tuna were sampled only once. These samples were also used in the substitution procedure, at times applied to a large catch (Table 7).

The effects of our substitution procedure and single samples on the estimated length composition of the catch were examined with the 1970 data. In that year, sampling coverage was poorest. In Figures 6 and 7, we show the estimated length composition by month using substitutions and also the portion of the composition derived from strata with two or more samples only. In general, the results indicate that substitutions affected

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[6] Champagnat, C., and R. Pianet. Croissance du patudo (*Thunnus obesus*) dans les regions de Dakar et de Pointe. Unpubl. manuscr., 7 p. Centre de Recherches Oceanographiques, B. P. 2241, Dakar, Senegal.

Table 7.—Number of NMFS area-month strata in which single samples were obtained or substituted.

Species - Year	Number of Strata[1]	Strata sampled once		Strata with one sample (including substitutions)	
		Number	Catch (tons)	Number	Catch (tons)
Yellowfin					
1968	5	1	140	2	1,100
1969	8	1	600	1	600
1970	13	1	490	2	2,260
1971	10	3	540	4	580
1972	19	2	390	4	420
1973	8	1	710	1	710
1974	17	1	190	2	260
Skipjack					
1968	6	2	640	3	660
1969	8	2	200	3	210
1970	12	0	0	0	0
1971	9	3	1,810	3	1,810
1972	18	0	0	0	0
1973	8	0	0	0	0
1974	17	4	1,840	5	1,880

[1] Only strata in which a catch was made are included.

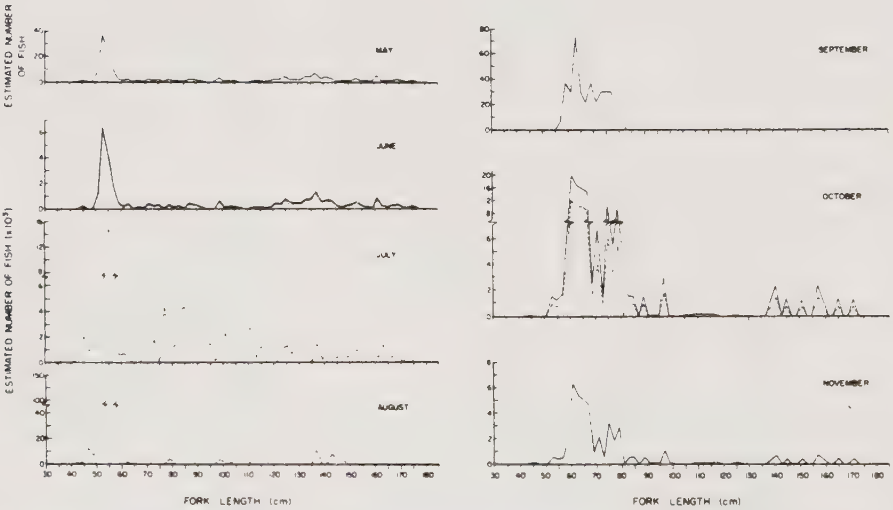
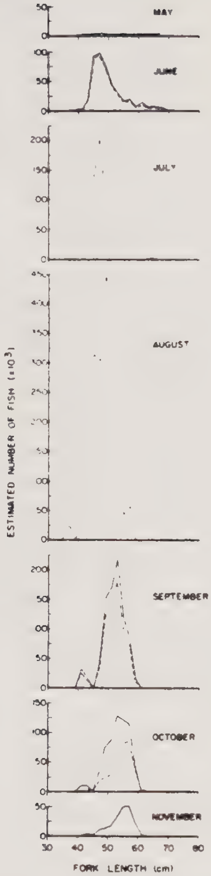


Figure 6.—Estimated length composition of yellowfin tuna by month caught by American seiners in 1970. (Solid line — stratified procedure with substituted samples; dashed line—stratified procedure without substituted samples and strata with one sample.)

Figure 7.—Estimated length composition of skipjack tuna by month caught by American seiners in 1970. (Solid line — stratified procedure with substituted samples; dashed line — stratified procedure without substituted samples and strata with one sample.)



principally the estimates of fish caught at the beginning (May) and end (September-November) of the 1970 fishing season. The effects are greater for yellowfin tuna (Fig. 6) than for skipjack tuna (Fig. 7).

DISCUSSION

Estimates of length composition of the American catches of yellowfin and skipjack tunas from the eastern tropical Atlantic have been published in the data records of the International Commission for the Conservation of Atlantic Tunas (1973; 1974b, c). The published estimates were based on preliminary data on total catches and on a stratified procedure with unweighted samples; consequently, they underestimated the numbers of fish caught and are not comparable to our estimates. Our estimates were based on total catches and on weighted samples. We consider them to be more accurate than those published in the data records.

The stratified procedure was used in our study to gain greater precision in our estimates. However, in years when sampling coverage was poor, the stratified procedure probably was inappropriate and may have distorted the results. In such circumstances, the unstratified procedure may have been more appropriate. Estimates based on the unstratified procedure are shown by dashed lines in Figures 2 and 3.

The stratified procedure is the most desirable for estimating the size composition of the catch of tunas because it can result in precise estimates (Hennemuth 1957). The choice between the unstratified and stratified procedures should be based on sampling cost as well as precision. For the American tuna catches from the eastern tropical Atlantic, the sampling cost is currently not much greater with the stratified than the unstratified procedure. The choice then is to use the stratified procedure which can account for area-time differences in the sizes of fish caught. If the sampling coverage is poor, however, particularly for yellowfin tuna with a wide range of sizes, the full advantage of the stratified procedure is lost and the estimates would not be very different from those based on the unstratified procedure. In this case, the procedures are equally precise in estimating the size composition of the catch and either procedure can be used without fear of losing more precision from one than the other.

ACKNOWLEDGMENTS

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ppendix Table 1.– Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1968.

Midpoint length (cm)	Number of fish by month		
	Aug.	Sept.	Oct.
59.0	1143	1948	0
61.0	2644	9460	0
63.0	8583	20216	7688
65.0	7313	16765	25628
67.0	5043	21756	23065
69.0	3861	3868	15377
71.0	2050	8371	5126
73.0	3570	7177	5126
75.0	1286	9878	5126
77.0	26	5672	2563
79.0	1561	2726	0
81.0	1479	777	2563
83.0	2061	1891	2563
85.0	877	2178	5126
87.0	83	1113	5126
89.0	480	6412	0
91.0	500	1737	7688
93.0	21	1886	5126
95.0	21	187	0
97.0	1041	717	2563
99.0	26	0	2563
101.0	0	0	5126
103.0	0	336	0
105.0	0	0	0
107.0	582	706	0
109.0	0	0	0
111.0	230	706	0
113.0	661	0	0
115.0	440	243	0
117.0	10	94	0
119.0	0	0	0
121.0	5	275	0
123.0	5	66	0
125.0	0	243	0
127.0	453	628	0
129.0	443	611	0
131.0	318	1782	0
133.0	518	2449	0
135.0	853	3534	0
137.0	2478	2883	0
139.0	351	2583	0
141.0	961	2469	0
143.0	1456	2517	0
145.0	3015	2021	0
147.0	2128	2077	0
149.0	766	1102	0
151.0	1882	1163	0
153.0	1772	1780	0
155.0	507	582	0
157.0	942	663	0
159.0	1539	872	0
161.0	902	517	0
163.0	762	681	0
165.0	399	196	0
167.0	1539	229	0
169.0	705	421	0
171.0	606	98	0
173.0	440	131	0
175.0	0	66	0
177.0	0	33	0
Total	71337	159492	128143

Appendix Table 2.– Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1969.

Midpoint length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
39.0	0	0	0	243	0
41.0	0	0	0	0	0
43.0	0	0	0	0	0
45.0	1100	0	146	0	0
47.0	1100	857	1583	0	0
49.0	1100	1501	1715	83	0
51.0	0	3672	146	1131	0
53.0	0	6002	0	2180	0
55.0	5502	4502	1467	83	0
57.0	9903	4502	1147	3311	0
59.0	16505	6002	858	12663	0
61.0	2201	7503	73	13712	0
63.0	1100	0	0	0	0
65.0	1100	0	0	1048	0
67.0	0	0	0	0	0
69.0	0	0	0	83	0
71.0	0	0	0	0	0
73.0	0	0	0	0	0
75.0	0	0	0	0	0
77.0	0	0	0	0	0
79.0	1100	0	0	0	0
81.0	0	0	0	0	0
83.0	0	0	0	0	0
85.0	0	0	0	0	0
87.0	0	0	0	0	0
89.0	0	0	0	0	0
91.0	0	0	721	0	0
93.0	0	0	0	0	0
95.0	0	0	721	0	0
97.0	0	993	0	0	0
99.0	0	0	721	0	0
101.0	0	0	0	0	0
103.0	1100	0	721	0	0
105.0	0	3429	1442	0	0
107.0	2201	15538	2163	0	0
109.0	1100	29220	8074	1362	0
111.0	2201	49690	5190	0	0
113.0	1100	48992	6716	3772	0
115.0	0	27385	5707	9150	317
117.0	0	12022	6200	12679	0
119.0	1100	7272	3655	19093	0
121.0	0	3346	7439	16464	0
123.0	0	6337	3444	10518	317
125.0	1100	7228	5542	6580	0
127.0	1100	4388	4776	5230	0
129.0	1100	3532	7087	2807	713
131.0	0	2099	10621	0	1030
133.0	1100	835	8333	83	1830
135.0	1100	1341	7489	1937	2695
137.0	0	186	3345	166	2695
139.0	0	0	2058	243	2061
141.0	0	1642	1149	326	2638
143.0	0	1188	3686	326	2507
145.0	0	929	2692	409	4575
147.0	0	1341	3417	1463	4222
149.0	0	671	2379	415	4444
151.0	0	0	2245	1297	4092
153.0	0	671	3087	569	5433
155.0	0	0	1349	811	4898
157.0	0	259	1924	984	3730
159.0	0	0	1273	1540	2832
161.0	0	0	563	1297	735
163.0	0	0	497	811	173
165.0	0	0	248	971	483
167.0	0	0	392	0	173
169.0	0	0	0	243	0
171.0	0	0	0	0	0
173.0	0	0	0	728	0
Total	55013	265075	134201	136811	52593

Appendix Table 3.- Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1970.

Midpoint length (cm)	Number of fish by month						
	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.
37.0	0	0	343	0	0	0	0
39.0	0	0	343	0	0	0	0
41.0	0	0	0	0	0	0	0
43.0	0	0	538	862	0	0	0
45.0	1	225	2135	862	0	49	16
47.0	0	0	881	12636	0	0	0
49.0	0	0	1076	5787	0	0	0
51.0	7	1222	2135	19562	0	0	0
53.0	37	6446	6565	38463	0	1456	466
55.0	24	4263	14769	143727	0	1208	387
57.0	10	1821	9606	147666	7427	1698	544
59.0	2	352	538	19331	37135	6729	2154
61.0	1	147	715	2586	29708	19557	6259
63.0	2	373	186	0	74269	16894	5407
65.0	0	0	0	0	29708	15986	5116
67.0	1	106	0	0	22281	14531	4651
69.0	0	0	343	0	37135	2664	852
71.0	2	386	715	0	22281	6686	2140
73.0	1	171	1774	0	29708	1456	466
75.0	2	260	0	0	29708	9941	3182
77.0	0	0	4292	0	29708	5526	1769
79.0	2	345	1774	3925	14854	9005	2882
81.0	1	106	1059	0	7427	0	0
83.0	1	246	3763	0	0	1456	466
85.0	0	0	4478	0	0	1504	481
87.0	2	400	1253	0	0	0	0
89.0	2	281	715	0	0	1456	466
91.0	1	171	687	0	0	49	16
93.0	0	0	881	0	0	0	0
95.0	0	0	1431	0	0	49	16
97.0	0	0	0	0	0	3008	963
99.0	3	559	687	3925	0	49	16
101.0	1	134	2312	0	0	0	0
103.0	1	150	1059	0	0	0	0
105.0	1	134	1597	3925	0	49	16
107.0	0	37	1059	7850	0	0	0
109.0	0	0	1940	3925	0	146	47
111.0	0	0	2833	0	0	146	47
113.0	1	134	343	0	0	97	31
115.0	1	106	1245	0	0	97	31
117.0	0	0	0	0	0	49	16
119.0	1	106	0	0	0	0	0
121.0	2	392	0	0	0	0	0
123.0	2	345	902	0	0	0	0
125.0	4	708	1253	0	0	49	16
127.0	2	350	538	0	0	0	0
129.0	2	407	1076	0	0	0	0
131.0	2	366	538	0	0	0	0
133.0	4	729	538	0	0	0	0
135.0	4	680	50	0	0	0	0
137.0	7	1294	1464	11774	0	0	0
139.0	3	492	237	0	0	1208	387
141.0	4	617	816	0	0	2319	742
143.0	3	583	795	7850	0	0	0
145.0	1	196	237	3925	0	1160	371
147.0	1	147	1147	3925	0	0	0
149.0	1	220	287	0	0	0	0
151.0	1	253	739	0	0	1160	371
153.0	3	504	910	0	0	0	0
155.0	1	155	50	0	0	0	0
157.0	1	147	473	0	0	2319	742
159.0	0	0	659	0	0	1160	371
161.0	5	820	252	0	0	0	0
163.0	1	248	1334	0	0	0	0
165.0	1	113	151	0	0	1160	371
167.0	1	239	403	0	0	0	0
169.0	2	260	151	0	0	0	0
171.0	1	98	50	0	0	1160	371
173.0	0	0	538	0	0	0	0
175.0	1	203	0	0	0	0	0
Total	168	29247	91658	442506	371349	133236	42645

Appendix Table 4.– Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1971.

Midpoint length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
37.0	0	1428	0	0	0
39.0	0	714	763	0	0
41.0	0	2496	11530	8309	2802
43.0	0	636	17676	15805	4987
45.0	1421	2183	11668	15071	4397
47.0	2131	5895	13291	10639	2903
49.0	710	7621	8928	4472	1166
51.0	0	3293	5066	809	273
53.0	4972	4046	4541	443	149
55.0	12786	6158	9779	6901	273
57.0	9234	12972	14705	18291	347
59.0	2131	5729	14545	17261	0
61.0	710	1692	11865	3268	75
63.0	0	591	6899	1015	0
65.0	0	409	2853	0	0
67.0	0	758	1710	0	0
69.0	0	419	0	0	0
71.0	1421	1265	493	0	0
73.0	0	718	245	0	0
75.0	0	678	490	0	0
77.0	0	510	914	0	0
79.0	0	556	843	0	0
81.0	0	219	735	0	0
83.0	0	563	1162	0	0
85.0	0	1069	1299	0	0
87.0	0	1732	1391	0	0
89.0	0	1403	2384	0	0
91.0	0	2618	4553	0	0
93.0	0	1339	2028	0	0
95.0	0	3418	2718	7	35
97.0	0	5424	1604	14	71
99.0	0	4072	3106	28	142
101.0	0	7294	2911	28	142
103.0	0	8177	1773	69	354
105.0	0	4192	1813	35	177
107.0	0	4847	713	42	212
109.0	0	1952	133	42	212
111.0	0	568	870	14	71
113.0	0	129	307	21	106
115.0	0	224	381	7	35
117.0	0	0	0	35	177
119.0	0	100	0	7	35
121.0	0	371	381	0	0
123.0	0	469	381	0	0
125.0	0	1026	0	0	0
127.0	0	759	381	0	0
129.0	0	503	232	0	0
131.0	0	414	1144	0	0
133.0	0	1033	1244	0	0
135.0	109	721	0	0	0
137.0	0	865	763	0	0
139.0	0	282	100	0	0
141.0	219	306	813	0	0
143.0	656	59	0	0	0
145.0	437	273	50	0	0
147.0	1421	451	431	0	0
149.0	437	290	0	0	0
151.0	219	183	945	0	0
153.0	219	339	0	0	0
155.0	219	431	0	0	0
157.0	547	1064	381	0	0
159.0	109	195	0	0	0
161.0	328	473	0	0	0
163.0	109	156	0	0	0
165.0	328	480	0	0	0
167.0	0	90	0	0	0
169.0	109	37	0	0	0
Total	40982	121377	175931	102633	19141

Appendix Table 5.– Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1972.

Midpoint length (cm)	Number of fish by month						
	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.
35.0	0	0	2287	0	0	0	0
37.0	0	0	3045	960	0	0	149
39.0	0	2580	[illegible]	0	0	0	149
41.0	0	0	2287	6715	0	8004	526
43.0	0	3893	3045	15300	8	25709	972
45.0	0	2580	5332	43939	8	7203	2379
47.0	0	0	2787	51155	1694	3910	2785
49.0	0	6473	[illegible]	50626	20265	5619	1574
51.0	0	9053	8551	47229	2199	3109	79
53.0	0	19419	4910	35526	513	10590	680
55.0	0	63651	34264	24288	6295	12941	747
57.0	0	55959	25452	62227	31511	26213	1398
59.0	0	28471	19040	49289	33396	25956	1338
61.0	0	2580	3977	36288	26814	11899	905
63.0	0	0	1516	10628	36	5041	1959
65.0	0	0	3045	5551	27	3477	1930
67.0	0	0	0	3239	27	2230	2656
69.0	0	0	5332	55	62	5087	3643
71.0	0	0	0	28	54	4460	680
73.0	0	0	175	0	108	8920	1358
75.0	0	0	0	28	102	8431	1673
77.0	0	0	2934	0	903	3345	2125
79.0	0	0	2287	0	407	0	1337
81.0	0	0	472	0	0	0	1474
83.0	0	0	2759	2943	127	0	1416
85.0	0	0	1230	148	815	0	788
87.0	0	0	1888	28	1538	1115	0
89.0	0	0	1524	1602	1410	2362	0
91.0	0	0	2575	380	1284	1208	394
93.0	0	0	1413	7070	468	1115	0
95.0	0	0	1993	2608	1003	1115	0
97.0	0	0	4183	6096	1804	1468	867
99.0	0	0	5680	2261	1466	3227	0
101.0	0	0	6474	8864	4435	3852	316
103.0	0	0	6811	6475	2554	742	237
105.0	0	0	2979	12280	3666	3203	395
107.0	0	0	1171	9518	5015	3715	316
109.0	0	0	175	11637	5462	4875	552
111.0	0	0	469	4511	1745	5332	79
113.0	0	0	175	7699	1070	5512	0
115.0	0	0	758	3068	268	2485	0
117.0	274	0	0	543	14	2138	0
119.0	91	0	588	55	8	3631	0
121.0	639	0	1710	28	498	2270	0
123.0	365	0	1826	712	0	116	0
125.0	1461	0	766	120	498	116	0
127.0	1369	0	647	515	14	1115	0
129.0	1735	0	766	55	142	2231	0
131.0	1096	0	2651	2200	21	1691	0
133.0	639	0	882	1022	12	1188	38
135.0	183	0	472	6931	23	2044	0
137.0	639	0	175	802	32	2620	113
139.0	183	0	766	2159	24	2677	0
141.0	0	0	0	1698	29	2411	0
143.0	183	0	0	609	6	569	192
145.0	0	0	0	570	3	280	189
147.0	91	0	0	1452	9	747	76
149.0	0	0	0	1255	4	475	113
151.0	91	0	294	1448	3	266	113
153.0	0	0	294	625	0	0	38
155.0	0	0	0	326	0	0	76
157.0	0	0	0	1649	3	266	189
159.0	0	0	0	850	0	0	151
161.0	0	0	0	375	3	266	227
163.0	91	0	294	2450	0	0	151
165.0	0	0	0	464	0	0	113
167.0	0	0	0	686	0	0	76
169.0	0	0	0	457	0	0	76
171.0	0	0	0	878	0	0	38
173.0	0	0	0	83	0	0	0
175.0	0	0	0	28	0	0	0
Total	9130	194659	199281	561304	159905	250587	39845

Appendix Table 6.- Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1973.

Midpoint Length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
39.0	93	4117	0	0	0
41.0	93	3937	1702	0	0
43.0	93	1372	6020	0	0
45.0	93	1372	2461	570	0
47.0	93	0	1838	285	0
49.0	0	0	1086	0	0
51.0	93	1372	443	0	0
53.0	374	6682	0	0	0
55.0	187	7874	344	0	0
57.0	374	14736	1439	0	0
59.0	654	9426	4687	0	0
61.0	374	16467	7773	285	0
63.0	374	6264	8116	0	0
65.0	93	8233	5791	856	0
67.0	0	1372	1131	0	0
69.0	0	2744	1131	285	0
71.0	0	1372	480	570	0
73.0	0	775	0	856	0
75.0	187	775	272	285	0
77.0	187	0	0	856	0
79.0	187	0	0	856	0
81.0	187	775	0	285	0
83.0	467	0	0	285	0
85.0	93	775	0	1141	0
87.0	93	0	0	285	0
89.0	187	775	0	781	0
91.0	0	0	959	736	0
93.0	93	775	0	285	0
95.0	0	775	0	1186	0
97.0	0	1549	480	1306	0
99.0	0	3873	959	1021	0
101.0	0	4648	959	736	1624
103.0	0	10845	480	901	2706
105.0	0	1549	0	0	1624
107.0	0	6438	0	1186	1082
109.0	286	775	0	165	2165
111.0	0	0	0	736	4871
113.0	0	0	0	165	5953
115.0	143	775	0	1488	3247
117.0	0	775	0	1323	2165
119.0	0	0	0	1488	541
121.0	429	0	959	662	0
123.0	428	775	0	165	541
125.0	1143	0	0	0	0
127.0	1428	0	0	165	0
129.0	1571	0	0	165	541
131.0	1001	0	0	0	0
133.0	1571	775	0	165	0
135.0	1858	775	0	0	0
137.0	1001	0	0	0	0
139.0	572	0	0	0	0
141.0	1144	1549	0	0	0
143.0	428	0	0	0	0
145.0	429	0	0	0	0
147.0	143	0	0	0	0
149.0	143	0	0	0	0
151.0	143	0	0	0	0
153.0	285	0	0	0	0
155.0	0	0	0	0	0
157.0	0	0	0	0	0
159.0	0	0	0	0	0
161.0	0	0	0	0	0
163.0	143	0	0	0	0
Total	18958	127866	49510	22525	27060

Appendix Table 7.—Estimated length composition of yellowfin tuna caught by American purse seiners in the eastern tropical Atlantic in 1974.

Midpoint Length (cm)	Number of fish by month									
	Jan.	Feb.	Mar.	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
35.0	0	0	0	0	0	87	33	540	0	0
37.0	0	0	0	0	0	87	0	0	0	0
39.0	0	0	0	0	0	745	132	2609	0	0
41.0	142	16	52	139	1893	174	33	540	1420	0
43.0	189	21	69	186	2524	793	0	0	5181	0
45.0	241	27	89	237	3218	928	66	1080	5430	0
47.0	73	8	27	72	978	1089	66	1080	1420	0
49.0	147	16	54	144	1956	875	99	1844	1420	0
51.0	121	13	44	118	1609	875	66	1753	1828	0
53.0	525	58	193	516	7003	349	66	1304	0	0
55.0	503	56	185	495	6719	1525	0	224	355	0
57.0	603	67	221	592	8044	2854	33	540	1118	0
59.0	366	41	135	360	4890	3734	66	2426	0	0
61.0	262	29	96	258	3502	2298	199	6606	4105	0
63.0	168	19	62	165	2240	770	298	9348	8024	0
65.0	73	8	27	72	978	652	199	7055	19749	0
67.0	73	8	27	72	978	910	33	1438	24512	0
69.0	0	0	0	0	0	257	33	540	8541	0
71.0	143	16	52	140	1906	201	33	764	3684	0
73.0	191	21	70	187	2544	772	0	0	8431	0
75.0	143	16	52	140	1906	1311	0	0	11579	0
77.0	96	11	35	94	1276	1218	0	0	6009	0
79.0	111	12	41	110	1488	2088	0	224	1766	0
81.0	118	13	43	116	1572	1141	296	4818	1105	0
83.0	276	31	102	272	3689	688	127	2065	760	0
85.0	138	15	51	136	1845	0	42	688	1901	0
87.0	290	32	107	285	3872	457	380	6194	380	0
89.0	274	30	101	269	3659	1028	253	4578	0	0
91.0	65	7	24	64	874	1336	211	3666	344	0
93.0	18	2	7	18	243	457	253	4578	0	0
95.0	16	2	6	16	213	201	42	688	0	0
97.0	32	4	12	31	425	288	0	0	0	0
99.0	34	4	13	34	455	370	42	688	355	235
101.0	138	15	51	136	1847	1208	42	913	344	0
103.0	65	7	24	64	874	1226	0	449	355	118
105.0	0	0	0	0	0	1378	0	449	355	118
107.0	236	26	87	232	3155	989	42	913	355	118
109.0	280	31	103	276	3744	2122	42	688	710	118
111.0	358	40	132	352	4785	3833	0	0	0	118
113.0	298	33	110	293	3979	2811	42	688	344	118
115.0	147	16	54	144	1956	4671	0	224	0	470
117.0	95	11	35	93	1262	4299	42	1137	0	353
119.0	139	15	51	136	1852	4800	108	2441	0	705
121.0	63	7	23	62	844	3131	0	1085	0	235
123.0	63	7	23	62	844	3232	33	1699	355	235
125.0	26	3	10	26	347	990	0	2468	355	353
127.0	50	6	18	49	661	87	33	3568	0	235
129.0	16	2	6	16	213	594	66	2239	0	235
131.0	18	2	7	18	243	663	42	688	355	0
133.0	0	0	0	0	0	707	0	374	0	118
135.0	2	0	1	2	30	292	0	187	355	0
137.0	5	1	2	4	61	436	42	1473	0	0
139.0	23	3	8	22	303	349	0	187	0	0
141.0	2	0	1	2	30	262	42	875	0	118
143.0	25	3	9	25	334	518	84	1750	0	0
145.0	20	2	8	20	273	493	0	187	0	353
147.0	18	2	7	18	243	349	0	0	0	470
149.0	5	1	2	4	61	117	0	411	0	705
151.0	14	2	5	13	182	466	0	0	0	0
153.0	11	1	4	11	152	292	0	0	0	235
155.0	5	1	2	4	61	0	0	224	0	0
157.0	11	1	4	11	152	174	0	0	0	0
159.0	0	0	0	0	0	0	0	0	0	0
161.0	9	1	3	9	121	0	0	0	0	118
163.0	5	1	2	4	61	87	0	0	0	0
165.0	2	0	1	2	30	0	0	0	0	0
167.0	5	1	2	4	61	0	0	0	0	0
169.0	5	1	2	4	61	0	0	0	0	0
171.0	0	0	0	0	0	0	0	0	0	0
173.0	2	0	1	2	30	0	0	0	0	0
Total	7592	845	2795	7458	101351	71134	3761	93195	123300	5881

Appendix Table 8.– Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1968.

Midpoint Length (cm)	Number of fish by month			
	Aug.	Sept.	Oct.	Nov.
39.0	0	0	2409	0
41.0	0	0	0	0
43.0	0	9257	2409	0
45.0	32798	70624	12046	0
47.0	131436	139866	68875	452
49.0	123675	91380	25709	362
51.0	28540	39476	22903	543
53.0	58833	21281	11452	271
55.0	45815	19055	27127	814
57.0	26035	28488	24718	814
59.0	25036	36659	11254	362
61.0	1752	34206	19900	814
63.0	0	9901	2211	90
65.0	1752	1076	0	0
Total	475672	501269	231013	4522

Appendix Table 9.– Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1969.

Midpoint length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
39.0	0	4739	1048	0	0
41.0	0	18759	7150	0	0
43.0	22468	51955	14148	2013	872
45.0	17653	57873	26569	5965	2617
47.0	17653	96038	25620	15956	7414
49.0	8024	65096	24959	32961	3489
51.0	4815	73737	24851	45359	2617
53.0	1605	147494	49613	48242	2181
55.0	4815	157306	54574	63066	2181
57.0	1605	91651	57854	59256	436
59.0	1605	54032	34425	46465	0
61.0	0	33216	15788	34248	0
63.0	0	7631	1925	10974	0
65.0	0	1431	0	2259	0
Total	80243	860958	338524	366764	21807

Appendix Table 10.– Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1970.

Midpoint length (cm)	Number of fish by month						
	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.
37.0	0	0	0	24835	0	0	0
39.0	0	0	4943	0	0	0	0
41.0	70	2446	12334	24835	32939	11349	0
43.0	548	19219	39089	149012	16469	11242	3355
45.0	2610	91520	135299	311362	0	2476	1492
47.0	2761	96812	206739	301012	41173	32304	10918
49.0	2128	74613	91742	442347	151716	75504	13999
51.0	1259	44155	67015	381942	170979	87829	17427
53.0	737	25827	35296	250967	218438	128026	31797
55.0	426	14935	14286	41588	121571	123720	49316
57.0	525	18418	7986	56027	87236	115101	51251
59.0	162	5666	8398	0	17866	46369	24234
61.0	391	13692	13004	0	0	2141	1290
63.0	114	3983	1844	0	0	0	0
65.0	177	6212	0	0	0	0	0
67.0	108	3789	0	0	0	0	0
Total	12016	421287	637975	1983927	858387	636061	205079

Appendix Table 11.– Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1971.

Midpoint length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
35.0	0	778	0	3879	0
37.0	0	1054	13973	10622	0
39.0	1715	1969	79921	87724	22140
41.0	5358	2552	423894	572735	27721
43.0	37829	11730	601535	591718	99537
45.0	80052	62618	921515	389419	135261
47.0	47581	94475	612368	533072	126521
49.0	18539	91279	361004	220877	120755
51.0	14683	97721	384174	313773	57679
53.0	4394	68150	155941	355220	54889
55.0	6109	25970	70307	236933	32933
57.0	0	10751	21632	90572	10978
59.0	0	2250	19227	20129	0
61.0	1715	1969	4787	0	0
63.0	0	0	3722	0	0
65.0	1715	864	0	0	0
Total	219690	474130	3674000	3426673	688414

Appendix Table 12.– Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1972.

Midpoint length (cm)	Number of fish by month						
	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.
33.0	0	0	2275	0	0	0	1290
35.0	2659	4106	42896	11985	0	8569	9871
37.0	5548	4646	44684	305230	100456	64367	70298
39.0	13525	13833	56322	497974	244828	206845	54401
41.0	22888	27127	64237	335621	391793	233145	33312
43.0	46122	50895	89352	231361	277366	109356	15386
45.0	63232	38305	278838	367061	300561	128683	14973
47.0	29478	86480	268123	279298	301074	179767	26969
49.0	2659	57565	126408	173796	111142	165454	26809
51.0	10636	61671	19085	59862	42428	113891	16855
53.0	2774	23297	22120	8954	30863	83770	11305
55.0	1387	4106	13263	2383	7122	27694	5450
57.0	0	14373	2275	9277	4748	15051	27
59.0	1387	8484	19586	0	0	3372	0
61.0	0	2323	26671	1711	0	2984	0
63.0	0	0	9360	0	0	0	0
Total	202295	397211	1085495	2284513	1812381	1342948	286946

Appendix Table 13.— Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1973.

Midpoint length (cm)	Number of fish by month				
	Jul.	Aug.	Sept.	Oct.	Nov.
33.0	126	3696	0	0	0
35.0	114	3340	0	5663	0
37.0	2151	62958	26879	3935	0
39.0	5594	163760	147907	21511	0
41.0	16286	476786	688219	185781	0
43.0	28982	848494	1392101	317625	0
45.0	31955	935517	2028754	478645	0
47.0	24474	716497	1518342	630823	1108
49.0	13104	383647	706955	388533	1582
51.0	3372	98730	133770	177279	4021
53.0	423	12382	11543	45677	5748
55.0	206	6024	0	2819	7422
57.0	299	8747	9252	0	4800
59.0	0	0	0	0	1399
61.0	68	1998	0	0	291
Total	127154	3722576	6663722	2258291	26371

Appendix Table 14.— Estimated length composition of skipjack tuna caught by American purse seiners in the eastern tropical Atlantic in 1974.

Midpoint Length (cm)	Number of fish by month									
	Jan.	Feb.	Mar.	Jun.	Jul	Aug	Sept.	Oct.	Nov.	Dec.
29.0	0	0	0	0	0	0	22682	0	0	0
31.0	0	0	0	0	0	0	56705	0	0	0
33.0	0	0	0	0	0	443	56705	0	0	0
35.0	0	0	0	0	0	0	317157	0	0	0
37.0	214	15	116	282	2002	0	458035	9524	0	8228
39.0	2399	174	1304	3164	22462	19659	425648	11547	6739	38798
41.0	6191	448	3365	8164	57965	38702	767286	415456	25499	207593
43.0	6602	478	3588	8705	61805	121033	680598	631623	75404	236729
45.0	5710	414	3103	7529	53455	102638	455170	208315	69577	260544
47.0	17511	1268	9517	23091	163939	102108	507089	300723	65934	243426
49.0	6597	478	3585	8699	61760	74915	262163	128828	115659	123428
51.0	11755	851	6389	15501	110056	105090	172428	27220	72673	55381
53.0	1254	91	682	1654	11743	30830	437149	0	26957	31378
55.0	264	19	144	348	2472	18203	502969	0	47175	27108
57.0	950	69	516	1252	8892	12519	318003	0	6739	22506
59.0	963	70	524	1270	9018	10518	118255	0	6739	12866
61.0	0	0	0	0	0	5786	44346	0	0	0
63.0	97	7	53	128	908	2384	14782	0	0	0
65.0	963	70	524	1270	9018	795	0	0	0	0
67.0	915	66	497	1206	8564	0	0	0	0	0
Total	62385	4518	33907	82263	584059	645623	5617170	1733236	519095	1267985

Appendix Table 15.— Estimated length composition of bigeye tuna caught by American purse seiners in the eastern tropical Atlantic.

Midpoint Length (cm)	Number of fish by year				
	1968	1971	1972	1973	1974
39.0	0	0	0	70	126
41.0	0	315	0	140	478
43.0	22	567	0	0	353
45.0	0	158	0	0	364
47.0	0	166	0	0	655
49.0	0	329	0	0	496
51.0	0	0	204	140	227
53.0	0	175	392	71	642
55.0		175	1794	211	914
57.0	0	1032	2390	493	787
59.0	0	1449	5163	1262	581
61.0	22	175	8116	1546	2372
63.0	0	420	3972	848	2517
65.0	0	646	1191	992	2187
67.0	44	158	400	284	792
69.0	22	472	0	284	1342
71.0	22	154	0	0	943
73.0	0	158	0	0	624
75.0	0	235	0	140	844
77 0	0	88	0	213	738
79.0	0	0	0	210	304
81.0	0	0	0	281	738
83.0	0	79	196	70	1477
85.0	22	0	204	282	1463
87.0	44	77	604	421	2070
89.0	44	158	400	417	643
91.0	0	79	799	701	867
93.0	0	312	791	566	1240
95.0	22	235	1574	142	661
97.0	0	471	196	142	204
99.0	0	548	196	71	325
101.0	0	236	587	0	394
103.0	0	315	0	0	482
105.0	0	166	0	71	238
107.0	0	245	0	0	41
109.0	0	235	0	0	755
111.0	0	465	0	71	430
113.0	26	954	0	0	1624
115.0	26	469	0	71	1028
117.0	26	940	0	0	1186
119.0	0	1656	0	71	803
121.0	26	1179	0	0	388
123.0	0	866	0	0	364
125.0	26	630	0	71	172
127.0	26	550	0	71	107
129.0	0	235	196	0	107
131.0	26	0	0	0	41
133.0	26	77	0	0	705
135.0	26	0	0	0	315
137.0	0	0	0	0	344
139.0	0	77	0	0	41
141.0	0	0	0	0	587
143.0	0	158	0	71	376
145.0	0	0	0	71	842
147.0	0	156	0	71	270
149.0	0	79	0	0	1079
151.0	0	232	0	0	0
153.0	0	77	0	0	235
155.0	0	232	0	0	0
157.0	26	0	0	0	0
159.0	0	154	0	0	0
161.0	0	154	0	0	41
163.0	0	0	0	0	0
165.0	0	77	0	0	0
167.0	0	154	0	0	0
169.0	0	0	0	0	0
171.0	0	88	0	0	270
Total	524	19687	29365	10636	41239

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GROWTH OF LABORATORY-REARED NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, FROM SOUTHERN CALIFORNIA

Gary T. Sakagawa and Makoto Kimura[1]

ABSTRACT

The northern anchovy, *Engraulis mordax*, was experimentally reared in the laboratory at the Southwest Fisheries Center, La Jolla, Calif. Data from three experiments were used to empirically fit a two-phase Gompertz growth model. The model describes growth from hatching to about 20 mo of age. It was estimated that the average length of laboratory-reared anchovies is 102 mm at 1 yr old and 119 mm at 2 yr old. Growth of laboratory-reared anchovies was comparable to that of anchovies in the wild.

Attempts to rear the northern anchovy, *Engraulis mordax*, at the Southwest Fisheries Center (SWFC), La Jolla, Calif., were begun in 1966 when G. O. Schumann collected anchovy larvae in the ocean off La Jolla and successfully reared them using wild plankton as food in the laboratory (Bardach 1968). Schumann's success was followed by other laboratory experiments in which anchovies were reared from eggs, larvae, and juveniles that were caught in the ocean (Table 1). In 1970, Leong (1971) developed a method for artificially inducing anchovies to spawn by controlling the photoperiod and injecting hormones. This technique is currently used at the SWFC to produce eggs and to rear anchovies for experimental purposes.

One of the purposes of the rearing experiments at the SWFC has been to obtain physiological and biochemical information needed for describing the energy budget of the northern anchovy, and to relate the results to the feeding dynamics of the anchovy population in the California Current, which consists of primarily young fish less than 3 yr old. Growth data are needed for analysis of the budget, and various attempts have been made to measure growth in the laboratory. Kramer and Zweifel (1970) and Lasker et al. (1970) reported growth rates of anchovy larvae. In this report we extend their analyses to include growth from hatching to about 20 mo old. We also present a mathematical model that describes this growth and compare our results with those of other investigators.

SOURCES OF DATA

Data primarily from experiments of G. O. Schumann (Schumann-I; Schumann-II), G. O. Schumann and A. Saraspe (Schumann-III), and R. Leong (pers. commun., SWFC) were used in our study (Table 1).

Schumann-II successfully reared larval anchovies for 22 days at about 22°C water temperature, which is higher than the temperature (15° to 16°C) at which anchovy larvae are frequently found in large numbers in the California Current (pers. commun., P. Smith, SWFC). The larvae were fed wild plankton and samples were taken for length measurement approximately daily.

Schumann-III reared anchovies from the egg stage through the juvenile stage in aquaria for 83 days on a diet of wild plankton, *Artemia salina*, and commercial trout food. The experiment was conducted from March to June and the water temperatures in the aquaria were not recorded. However, during March to June the average water temperature in rearing aquaria at the SWFC is generally about 18° to 22°C.

Leong (pers. commun.) obtained juvenile anchovies from a live-bait dealer and reared the fish to maturity in a 4.6-m diameter pool (13.2 kl) with circulating seawater. The water temperature in the pool was a few degrees higher than the prevailing water temperature off Scripps Pier, La Jolla, site of the water intake for the experimental pool (Lasker and Vlymen 1969). Leong fed the fish a diet of *Artemia salina,* ground squid and anchovies, and commercial trout food. Once a month about 25 fish were sacrificed for length and weight measurements.

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TABLE 1. — Laboratory experiments of rearing the northern anchovy at the Southwest Fisheries Center, La Jolla, Calif.

Source	Life stage at start	Start of rearing	Rearing duration (days)	Average length (mm)		Food
				Start	Finish	
Hunter (1976)	Eggs	April	74	4.0	35.0	*Gymnodinium splendens, Brachionus plicatilis, Tisbe furcata,* and *Artemia salina*
Kramer and Zweifel (1970)	Eggs	August and September	35	3.2	17.4	Wild plankton and *A. salina*
Lasker et al. (1970)	Eggs	February	50	3.4	21.0	*Bulla gouldiana, G. splendens,* and *A. salina*
Leong (unpubl. data)[1]	Juveniles	April	474	88.3	117.7	Squid, anchovy, *A. salina,* and trout food
Paloma (see text footnote 3)	Juveniles	November	624	75.0	106.2	*Artemia salina* and trout food
Schumann-I (G. O. Schumann unpubl. data)[2]	Larvae	March	97	18.0	81.9	Wild plankton
Schumann-II (Kramer and Zweifel 1970)	Eggs	March	22	2.9	16.2	Wild plankton
Schumann-III (G. O. Schumann and A. Saraspe unpubl. data)[2]	Eggs	March	83	3.5	67.1	Wild plankton, *A. salina,* and trout food
Theilacker and McMaster (1971)	Eggs	—	19	—	12.0	*Gymnodinium splendens, B. plicatilis,* and *A. salina*

[1] Pers. commun., Southwest Fisheries Center, La Jolla, Calif.
[2] Data are on file at the Southwest Fisheries Center, La Jolla, Calif.

In all of these experiments the fish were from the southern California stock (Vrooman and Smith 1971), reared at laboratory ambient water temperature, and not subjected to experimental treatment or excessive handling. All fish sampled for measurements were sacrificed. The length measurement is standard length.

TREATMENT OF DATA

The age of anchovies reared by Schumann-II and Schumann-III were known because the anchovies were hatched from eggs at the start of the rearing experiments. In Leong's (pers. commun.) experiment, the exact age of his fish was not known because juvenile fish of average length of 88.3 mm were used at the start of the experiment. We estimated the age of Leong's fish from data from Schumann-I in which anchovies were reared for 97 days from an average length of 18.0 to 81.9 mm (Table 1), and data from Schumann-III which indicated that an 18.0 mm fish, raised from eggs, was about 30 days old. Our age estimate is 4 mo.

Several mathematical models describing growth of organisms are available (e.g., Parker and Larkin 1959; Richards 1959; Laird 1969). The commonly used models in fisheries are the exponential, the von Bertalanffy, and the Gompertz models (Beverton and Holt 1957; Silliman 1969). The Gompertz model was selected for our study because it was shown by Kramer and Zweifel (1970) to be better than the exponential model for describing growth of laboratory-reared anchovy larvae and because it generally describes the growth of fishes fairly well. Also, preliminary analysis of our data indicated that the von Bertalanffy model poorly described the growth of young fish.

The Laird version of the Gompertz growth model (Laird 1969) describes an asymmetric sigmoid curve of the form.

$$L_t = L_0 \exp \left\{C \left[1 - \exp(-at)\right]\right\}$$

where L_0 = length at zero age or hatching
C = a constant
a = rate of decay of exponential growth
t = age in months.

This model was fitted to our data using an iterative least squares procedure (Conway et al. 1970). Our goal was to describe growth on a coarse time scale, i.e., monthly rather than on a fine time scale, i.e., daily.

GROWTH FROM HATCHING TO JUVENILE STAGE

The Gompertz growth model and an exponential growth model were applied to data of Schumann-II by Kramer and Zweifel (1970). Both models described the data from Schumann-II reasonably well, although the Gompertz model described the data better. In the Kramer-Zweifel analysis the length at zero age, L_0, was fixed at 2.5 mm, the average size at hatching. We also applied the Gompertz growth model to data of Schumann-II. Kramer and Zweifel (1970) used data only for 17 days of growth. We used all of the data of Schumann-II, which included sampling through 22 days of growth, and fitted the model first with L_0 fixed at 2.5 mm and again without this constraint, i.e., L_0 was estimated. The results (Figure 1) indicate that there is not much difference in the curves with L_0 fixed or estimated within the range of the data. Outside the range of the data, the curves diverge considerably and there is a substantial difference; the curve with L_0 estimated has a lower asymptotic length (61 mm) than the curve with L_0 fixed at 2.5 mm (asymptotic length of about 696 mm).

Zweifel and Lasker[2] showed that a two-phase Gompertz curve described the data from Schumann-II better than a single-phase Gompertz curve. The separation of the phases occurred at about 6 days of age, the onset of feeding in anchovy larvae.

Schumann-III reared anchovies for a longer period than Schumann-II. Fish reared by Schumann-II, however, were larger than those reared by Schumann-III at similar ages. For example, at 0.5 mo of age fish reared by Schumann-II averaged 12.1 mm long and fish reared by Schumann-III, 8.2 mm long. Although the sample size is small, this difference is statistically significant at the 1% probability level. Differences in rearing procedures, i.e., diet and temperature of water, probably produced the difference in growth (Kramer and Zweifel 1970; Lasker et al. 1970).

The Gompertz growth model was applied to data from Schumann-III first with L_0 fixed at 2.5 mm and then with L_0 estimated (Figure 2). As in the case with data from Schumann-II, this model describes the growth data reasonably well, and the curve with L_0 estimated has a lower asymptotic length (81 mm) than the curve with L_0 fixed (asymptotic length of about 93 mm).

GROWTH DURING JUVENILE TO ADULT STAGE

Anchovies reared by Leong (pers. commun.) were juveniles at the start of the experiment and grew to an average size of 117.7 mm in 474 days (Table 2). Growth was in steplike stages characterized by rapid growth followed by a leveling off. The first stage was between 4 and 12 mo of age and the second was between 12 and about 20 mo of age.

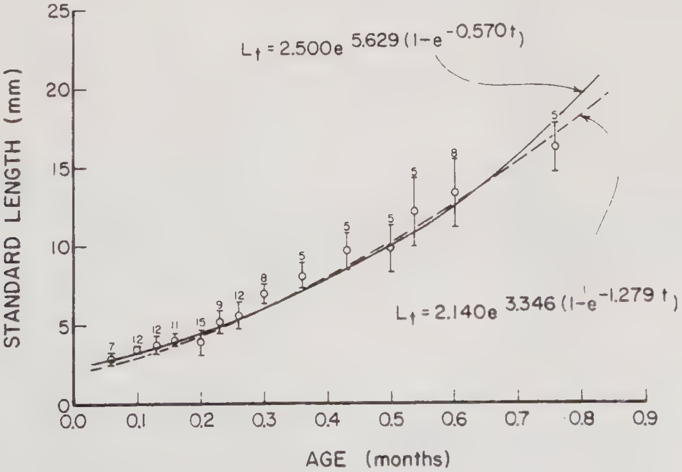

FIGURE 1.—Growth of anchovy larvae reared in the laboratory. The Gompertz growth model of the form, $L_t = L_0 \exp\{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm and broken line is based on L_0 estimated, 2.140 mm. Data from Schumann-II (Kramer and Zweifel 1970). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

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[2] Zweifel, J. R. and R. Lasker. 1974. Prenatal and postnatal growth of fishes—a general model. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

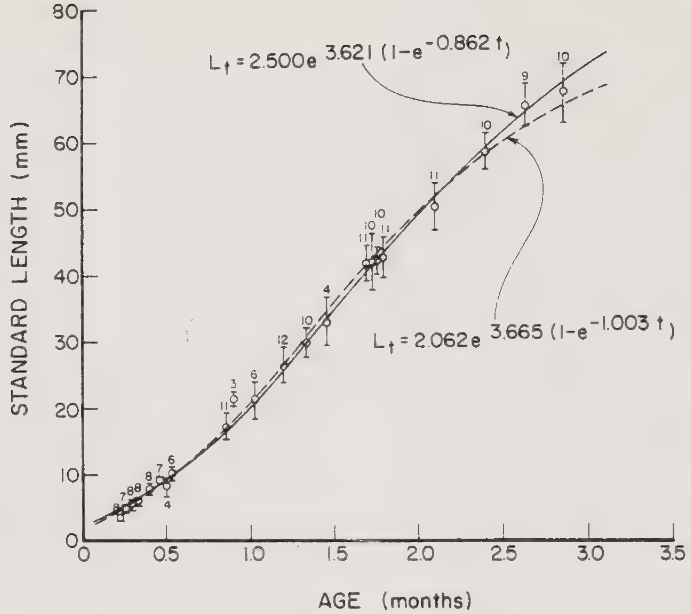

FIGURE 2.—Growth of anchovy reared in the laboratory. The Gompertz growth model of the form $L_t = L_0 \exp\{C[1 - \exp(-at)]\}$ is used to describe the data. Solid line is based on L_0 fixed at 2.500 mm, and broken line is based on L_0 estimated, 2.062 mm. Data from Schumann-III (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown.

TABLE 2.—Estimated age and average standard length of northern anchovies reared in the laboratory by R. Leong (pers. commun., Southwest Fisheries Center, La Jolla, Calif.)

Age		Number of fish	Average length (mm)	Standard deviation
Days	Months			
120	4.00	10	88.30	6.34
153	5.10	23	92.35	4.90
189	6.30	24	94.63	5.85
231	7.70	25	97.68	6.40
270	9.00	25	96.48	6.19
301	10.03	23	99.30	5.14
351	11.70	25	101.52	4.59
385	12.83	25	105.72	5.26
413	13.77	25	109.16	5.75
444	14.80	26	109.23	6.07
471	15.70	26	110.58	6.82
503	16.77	25	114.56	6.57
533	17.77	24	117.38	6.11
562	18.73	25	116.32	7.07
594	19.80	25	117.68	6.69

The Gompertz growth model was applied, but did not adequately fit the data. This is characteristic of asymptotic models like the Gompertz model when all the data points are for a segment of the growth curve where growth is relatively slow and the plot of the data exhibits little curvature.

GROWTH FROM HATCHING TO ADULT STAGE

Growth Curve

As indicated earlier, anchovies reared by Shumann-III grew slightly faster than those of Schumann-II, probably due to slight differences in the rearing environment and procedures. Because our goal was to construct a general growth curve and the differences in the data were relatively slight, we elected to disregard the difference and pooled the data from the three experiments (Schumann-II, Schumann-III, and Leong). The Gompertz growth model was applied to the pooled data. The results (Figure 3) indicate that the model does not adequately describe the data. For example, the model overestimates the sizes of fish at about 4 to 12 mo old and underestimates the sizes of fish older than about 13 mo. These biases are caused by the steplike growth pattern which produces plateaus at about 6 mo and 19 mo of age.

To account for this steplike growth pattern, a

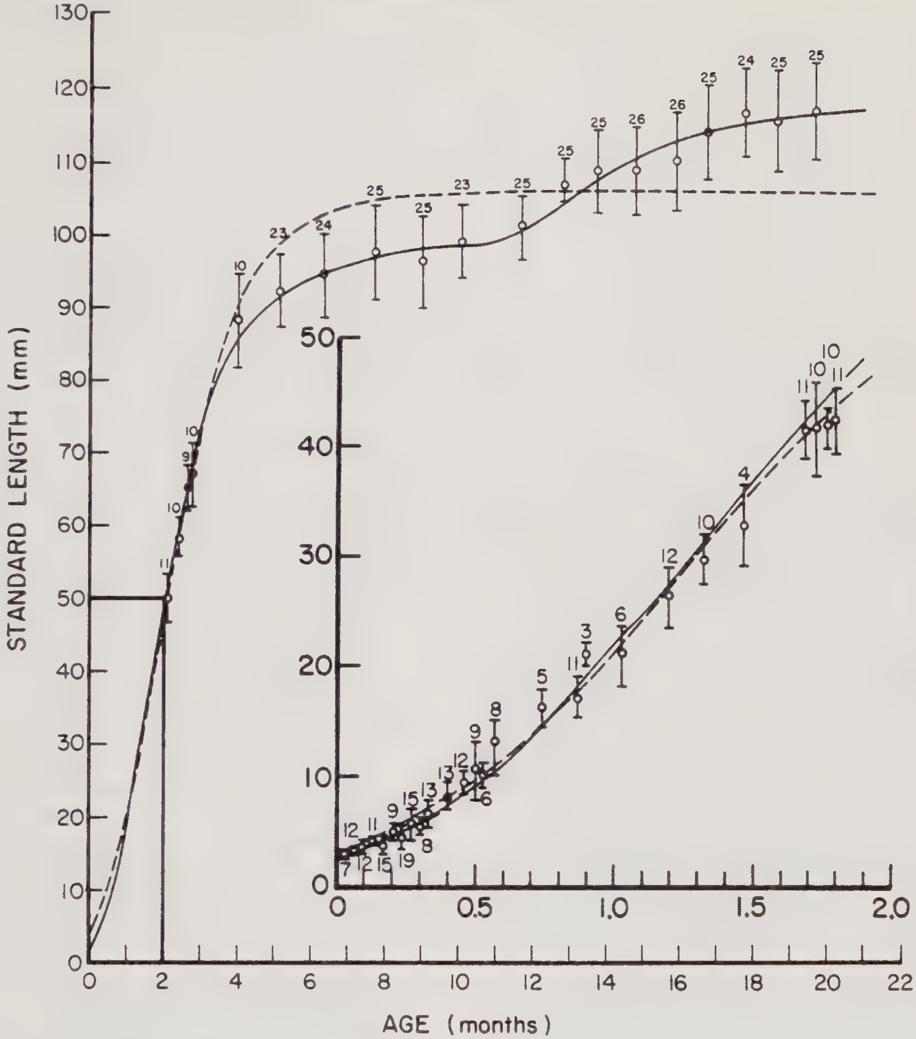

FIGURE 3.—Growth of northern anchovy reared in the laboratory. One-phase (broken line) and two-phase (solid line) Gompertz growth models are used to describe the data. Data from Schumann-II (Kramer and Zweifel 1970), Schumann-III, and Leong (unpubl. data, Southwest Fisheries Center, La Jolla, Calif.). The mean (circle), one standard deviation on each side of the mean, and sample size are shown. Broken line is described by $L_t = 2.825 \exp \{3.623 [1 - \exp(-2.877t)]\}$ and solid line by $L_t = 2.745 \exp \{3.563 [1 - \exp(-0.848t)]\}$ for $t \leq 11$ mo, and $L_{(t-11)} = 96.782 \exp \{0.213 [1 - \exp(-0.258 \{t - 11\})]\}$ for $t > 11$ mo.

two-phase Gompertz model (Zweifel and Lasker see footnote 2) was fitted to the data. The two-phase model is essentially two separate Gompertz equations that describe different segments of the growth curve. The equations were fitted simultaneously and the convergence point of the equations was determined on the basis of least squares analysis. Our best fit of the data was with the equation, $L_t = 2.745 \exp \{3.563 [1 - \exp(-0.848t)]\}$ for growth from hatching to 11 mo of age and the equation, $L_{(t-11)} = 96.782 \exp \{0.213 [1 - \exp(-0.258 \{t - 11\})]\}$ for growth from 11 to 20 mo of age (Figure 3). From the equations, the estimated average length of anchovies after 1 yr of life is 101.6 mm and after 2 yr of life, 118.9 mm (Table 3).

TABLE 3.—Estimated growth for the first 24 mo of life of the northern anchovy reared in the laboratory. Estimates are based on a two-phase Gompertz growth curve (see text).

Age (mo)	Standard length (mm)	Age (mo)	Standard length (mm)
hatching	2.7	13	105.5
1	21.0	14	108.6
2	50.4	15	111.0
3	73.2	16	112.9
4	85.9	17	114.5
5	92.0	18	115.6
6	94.7	19	116.6
7	95.9	20	117.3
8	96.4	21	117.8
9	96.6	22	118.3
10	96.7	23	118.6
11	96.8	24	118.9
12	101.6		

General Remarks

The steplike growth pattern is commonly found in fishes. Gerking (1967) reviewed the literature on this subject and noted that many temperate species have seasonal, sigmoid growth curves. Lockwood (1974) recognized this feature in the growth of plaice and brown trout and applied a multiphase von Bertalanffy growth model to describe the data mathematically. His results were satisfactory but because the von Bertalanffy growth equation does not describe a sigmoid curve, his analysis was confined to growth for part of the season only.

In this study we used the Gompertz growth equation to describe the sigmoid curve. The two-phase model satisfactorily described our data for laboratory-reared anchovy, and a cycle that occurs at 12-mo intervals is evident in our results. This is quite similar to the seasonal growth patterns described by Gerking (1967), Mann (1971), Kroger et al. (1974), and others. The cycle indicates that for the northern anchovy, about 95% of the first year's growth is completed by the 8th month of life and about 91% of the second year's growth is completed by the 20th month of life.

If this cyclic pattern in growth also occurs in anchovies in the wild, then it may have a considerable impact on yield models, such as yield-per-recruit models, and on management decisions. It might be that the best harvesting strategy in terms of maximum yield-per-recruit is during the period of the cycle when growth is relatively slow, i.e., period of plateau. It seems important, therefore, that a multiphase growth function be considered for use in yield models for northern anchovy.

We point out the possibility that the cyclic pattern could have been artificially created because our data were from three cohorts that were reared under different laboratory conditions during different periods of the year and the ages of fish reared by Leong (pers. commun.) were estimated. However, we discount that possibility because the cyclic pattern persists even if our age estimates of Leong's fish were off by 1 or 2 mo. Rearing conditions, on the other hand, could have produced the cyclic pattern if the pattern is influenced primarily by environmental factors, e.g., temperature, length of day, and food density and quality.

WEIGHT-LENGTH RELATION

Weight-length relations for the northern anchovy were reported by several investigators (Table 4). Only Lasker et al. (1970), however, reported on estimates for laboratory-reared anchovies, and their estimates were for anchovy larvae.

Length and weight data were collected by Leong (pers. commun.) and Paloma[3] from fish reared in their experiments. We used their data from 757 fish to estimate the weight-length relation of laboratory-reared anchovies of 70 to 131 mm long. Data from Paloma were only from fish in their first year of life, in which growth was somewhat similar to that of fish reared by Leong. Separate estimates were made for males and females (Table 4), and the results subjected to covariance analysis (with log transformed data) to test whether the relation could be represented by a single line. The analysis indicated that the separate lines were parallel and not significantly different from a common line. The data were, therefore, pooled and a weight-length relation estimated for the combined (all sexes) data (Table 4).

Our estimates are compared with those of Collins (1969) for anchovies from southern California (Figure 4). Collins based his estimates on data from anchovies caught in the reduction fishery off southern California. For a given length, fish examined by Collins were lighter than the laboratory-reared fish. This phenomenon appears common for fishes (Kramer 1969; Kimura and Sakagawa 1972). Kimura and Sakagawa (1972) mentioned that for Pacific sardines, differences in diet and reduced amount of exercise because of confinement were some possible causes for

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[3] Paloma, P. 1971. Annulus formation in the scale of marked anchovy *Engraulis mordax* Girard. Unpubl. manuscr. Southwest Fisheries Center, La Jolla, CA 92038.

TABLE 4.—Coefficients of the weight-length relation for the northern anchovy as reported by various investigators. The coefficients are for the equation, weight = $a \times \text{length}^b$.

Origin of sample	Source	Rearing environment		Sex	Number of fish	b	a	Unit of measure		Range of length (mm)
		Ocean	Laboratory					Length	Weight	
Southern California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.453	2.7×10^{-4}	mm	ounce	56-134
	Collins (1969)	X		Male	926	3.049	8.1×10^{-6}	mm	gram	97-161
	Collins (1969)	X		Female	1,513	2.984	1.1×10^{-5}	mm	gram	
	Lasker et al. (1970)		X	Combined sexes	63	3.324	1.5×10^{-4}	mm	mg	3- 25
	Present study[2]		X	Male	257	3.521	1.0×10^{-6}	mm	gram	73-126
	Present study		X	Female	500	3.433	1.5×10^{-6}	mm	gram	70-131
	Present study		X	Combined sexes	757	3.461	1.4×10^{-6}	mm	gram	70-131
Central California	Clark and Phillips (1952)	X		Combined sexes	(1)	3.252	7.2×10^{-6}	mm	ounce	114-160
	Collins (1969)	X		Male	270	2.805	2.7×10^{-5}	mm	gram	80-171
	Collins (1969)	X		Female	407	2.743	3.6×10^{-5}	mm	gram	

[1] Clark and Phillips (1952) used data from 17 samples from southern California and 77 samples from central California but they did not specify the number of fish in each sample.

[2] Unpublished data from R. Leong and P. Paloma (pers. commun.), Southwest Fisheries Center, La Jolla, Calif. The coefficients with the more appropriate functional regression (Ricker 1973) are: 1) male, $a = 7.0 \times 10^{-7}$, $b = 3.608$; 2) female, $a = 1.0 \times 10^{-6}$, $b = 3.518$; 3) combined sexes, $a = 9.2 \times 10^{-7}$, $b = 3.547$.

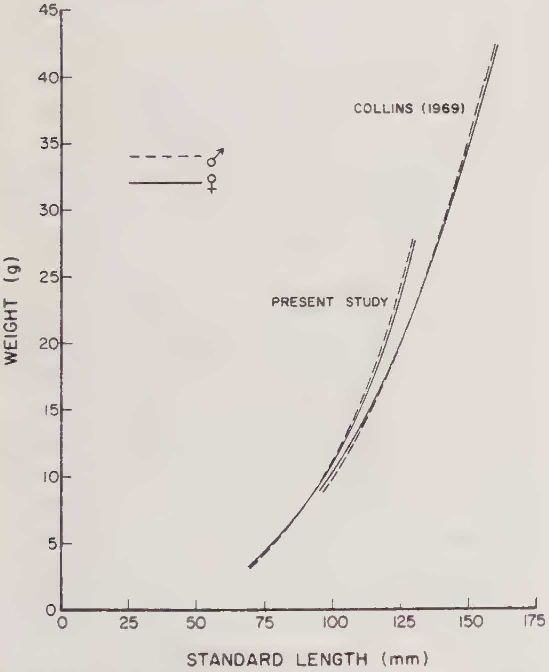

FIGURE 4. — Weight-length relation for northern anchovy from southern California. Laboratory-reared fish were used in present study, and fish caught in the California reduction fishery were used by Collins (1969).

laboratory-reared fish being heavier than fish in the wild. Zweifel and Lasker (see footnote 2) mentioned the possibility that the differences arise when the curves are based on fish in different phases of their growth cycle.

COMPARISONS OF GROWTH

Growth of anchovies reared in the laboratory was studied by Kramer and Zweifel (1970), Lasker et al. (1970), Theilacker and McMaster (1971), Hunter (1976), and Paloma (see footnote 3). Kramer and Zweifel and Lasker et al. studied the effects of diet and water temperature on growth of anchovy larvae. They concluded that larval growth was best at 22°C with wild plankton as a food source. The growth curve of Figure 3 for the larval stage is for fish reared on wild plankton and *Artemia salina* at about 22°C. It is the best so far attained in the laboratory.

Theilacker and McMaster (1971) and Hunter (1976) reared anchovy larvae on cultured foods. Results of their studies show that growth of anchovies on cultured food diets is about the same as that on wild plankton.

Paloma (see footnote 3) obtained juvenile anchovies from a live-bait dealer and reared the fish in the laboratory for 624 days (Table 1). He injected oxytetracycline hydrochloride into the fish at various times to label the body structures for ageing. At 2-wk intervals, scales and data on body measurements were collected. Fish reared by Paloma started at a smaller average size (75 mm long) than fish reared by Leong (pers. commun.) (88 mm long) and grew at a much slower rate (21 mm in about 470 days versus 30 mm in about 470 days for Leong's fish) without a noticeable steplike pattern. Perhaps the frequent handling, injection of tetracycline, and small size of the rearing pool (2.74-m diameter) contributed to the slow growth and eliminated the steplike pattern.

Clark and Phillips (1952), Miller et al. (1955), Collins (1969), and Collins and Spratt (1969), studied growth of anchovies caught in the California fisheries. They used scales and otoliths for ageing fish to the nearest whole year. Clark and Phillips reported their results for the combined southern and central California fisheries. Miller et al., Collins, and Collins and Spratt, on the other hand, reported their results separately for each fishery.

To compare growth of anchovies in the wild with that of laboratory-reared anchovies, we limited the comparison to fish from southern California to eliminate possible regional biases in growth. We also adjusted Miller et al.'s (1955) data upward by 1 yr to make them comparable to those of Collins (1969) and Collins and Spratt (1969) (Figure 5). This was necessary because Miller et al. did not correct their age readings for date of capture (August to March) and growth on the margin of the scale relative to the birthdate (April 1); hence, they underestimated the age of their fish by approximately 1 yr.

The growth curves in Figure 5 indicate that anchovies in the wild are 95 to 115 mm long at about 1 yr old and 115 to 125 mm long at about 2 yr old and possibly growth was slower in the 1960's than in the 1950's owing to the dramatic increase in the northern anchovy population (Spratt 1975). Our growth estimates for laboratory-reared anchovies are 102 mm for 1 yr olds and 119 mm for 2 yr olds; hence, growth of laboratory-reared fish seems to be similar to that of anchovies in the wild. However, we note that this direct comparison is not entirely valid because inherent biases exist in the growth curves in Figure 5. The biases exist because: 1) larger fish are generally more available to the reduction fishery than the live-bait fishery (Messersmith 1969) and thus are overrepresented in the data for the reduction fishery; 2) live-bait fishermen "consciously avoid taking large anchovies, since they are less desirable for bait than smaller anchovies" (MacCall 1973:5-6) and thus large fish are underrepresented in the data for the live-bait fishery; 3) the true birthdate of anchovies aged by otolith or scale readings is not known although it is known that the birth date varies (Kramer and Smith 1971; Smith 1972), the ages, therefore, are not exact ages; and 4) growth of several year classes are averaged and consequently, variability in growth is reduced.

Spratt (1975), who also studied growth of the northern anchovy from otoliths, accounted for some of these biases by using back-calculated lengths and fish from the reduction fishery, live-bait fishery, and catches of a research vessel. He estimated that the mean standard length of anchovies in the wild is 92 and 112 mm at the end of the first and second year of life, respectively. These estimates are somewhat less than ours for laboratory-reared fish but they are close.

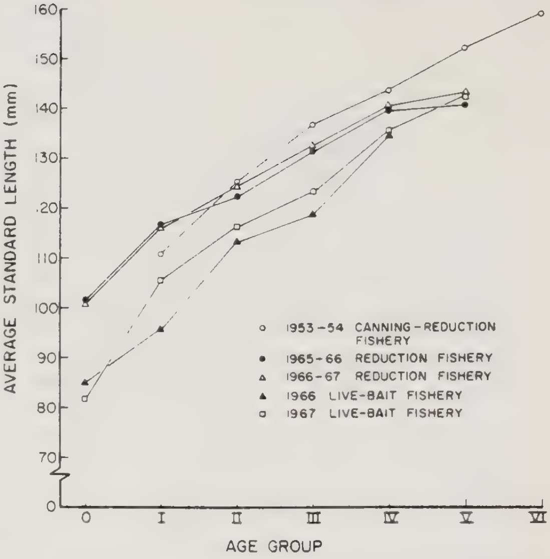

FIGURE 5.—Growth curves for northern anchovy caught off southern California in the fisheries for reduction (Collins 1969), live-bait (Collins and Spratt 1969), and canning-reduction (Miller et al. 1955).

It appears that growth of anchovies in the wild is similar to that estimated, on an annual basis, from our growth curve. We have not demonstrated, however, whether there is a cyclic pattern in growth of anchovies in the wild similar to that revealed in our results for laboratory-reared fish. On the other hand, studies on growth of other temperate fishes have shown that a seasonal cycle is common, which leads us to believe that a seasonal cycle exists for anchovies in the wild. The use of our growth curve for describing the feeding dynamics of northern anchovies of at least 2 yr of age in the California Current is therefore practical until a seasonal growth curve is described for anchovies in the wild.

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Zweifel read the manuscript and offered valuable comments and suggestions. Robson Collins and members of his staff at the California Department of Fish and Game read the manuscript and brought to our attention related studies that were in press.

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VON BERTALANFFY GROWTH CURVES FOR STRIPED MARLIN, *TETRAPTURUS AUDAX,* AND BLUE MARLIN, *MAKAIRA NIGRICANS,* IN THE CENTRAL NORTH PACIFIC OCEAN

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ABSTRACT

The growth of striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, was described by fitting von Bertalanffy growth curves (an assumed age model and a length-increment model) to the progression of age-groups, by quarters, through the Hawaiian longline fishery from 1960 to 1970. For striped marlin, the sexes grew at about the same rate and had similar predicted asymptotic maximum fork lengths, 277.4-314.4 cm for males and 288.7-326.2 cm for females. For blue marlin, the sexes grew at about the same rate until 250 cm. Above this length, the growth rate of males declined and an asymptotic maximum length of 298.8-368.0 cm was predicted. For females above 250 cm, the growth continued at a rapid rate; exhibiting little tendency toward an asymptote over the range of ages available to the study.

While blue marlin, *Makaira nigricans* Lacépède, are important in the U.S. sport fishery in California, Florida, and Hawaii and striped marlin, *Tetrapturus audax* (Philippi), are important in California and Hawaii, little is known about their population characteristics or parameters. In particular, growth of these species has received little attention. In this paper, the growth of striped and blue marlins is described by fitting von Bertalanffy growth curves to age-groups separated from length-frequency data collected in Hawaii.

A review of the literature revealed four papers dealing with the growth of marlins. In them, growth was examined by plotting the progression of mean sizes for age-groups separated from size-frequency data by month or some other time interval; the fitting of a functional growth model (e.g., von Bertalanffy or Gompertz) was not discussed or attempted. Royce (1957) studied striped marlin in the Hawaiian longline fishery (1949-52) and concluded that small (13.6-17.7 kg) and large (45.3-49.4 kg) size classes grew about 13.6 kg per year. De Sylva (1957) studied the growth of sailfish, *Istiophorus platypterus* (Shaw and Nodder), in the Atlantic from records obtained primarily from sport catches. His growth curve, fitted by eye, showed an extremely rapid rate of growth: 180 cm total length in the first year of life and 30 cm in the second. Maximum age was estimated as IV. De Sylva and Davis (1963) compared data for the white marlin *T. albidus* Poey, and the sailfish and concluded that white marlin live longer than sailfish. Koto and Kodama (1962), studying the growth of sailfish caught near Japan, found an annual growth of 35 cm for a 140-175 cm eye orbit-fork length group, 20 cm for a 176-195 cm group, and 15 cm for a 196-210 cm group.

The objective of this study was to quantitatively describe the growth of striped and blue marlins using a model that adequately followed the observed data and provided estimates of growth parameters, which could be incorporated into analytical models of population dynamics. Since the von Bertalanffy growth model satisfied these conditions, it was used in this study. Specifically for striped marlin, growth parameters were sought by sex for individual cohorts and then for data pooled over all years. For blue marlin, growth parameters were sought by sex only for data pooled over all years because the data were insufficient to work with individual cohorts. By pooling across years, the assumption was made that the populations under study were in or tending toward a steady state. As such, yearly variations in mean lengths of age-groups as well as variations in growth parameters between cohorts were treated as homogeneous sets of responses to variations in the environment.

MATERIALS

From April 1960 through April 1970 at the

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auction blocks of the fresh fish markets in Honolulu, the staff of the Honolulu Laboratory, National Marine Fisheries Service, NOAA, collected weight and sex data from large pelagic species caught by the Hawaiian longline fleet. Details of the longline fishery are given by June (1950) and Otsu (1954). All fish were weighed to the nearest whole pound. Due to the nearly complete utilization of marlin by the dealers, only a small incision could be made in the abdominal wall in order to examine the gonads. At best, a small section of gonad could be cut off and examined; no microscopic determinations were made. Thus, it is possible that some misidentification of the sex of these fish occurred, especially preceding sexual maturity for both species and following spawning for blue marlin.

METHOD OF ANALYSIS

Briefly, the analyses consisted of 1) transforming the data into usable form by (a) calculating length-weight relationships using functional regressions (Ricker 1973), (b) converting weights to lengths, and (c) grouping the lengths by sex, quarter, year, and length interval; 2) separating age-groups from the frequency distributions and estimating their mean lengths; 3) setting up the progressions of mean lengths and corresponding age structures; and 4) fitting von Bertalanffy growth models to the progressions of mean lengths. Following these steps, tests were performed to determine whether the yearly samples were homogeneous and could be pooled. These tests consisted of a series of nonparametric Friedman two-way analyses of variance (Hollander and Wolfe 1973:139) performed on the number of age-groups, the mean lengths of age-groups, and the percent representation of age-groups separated for each year sampled, as well as on the growth parameters of the different cohorts. Also, a sign test (Siegel 1956:68) was used to test for trends in mean length between sexes; and a series of one sample runs tests (Siegel 1956:52) was used to test for trends in mean length among cohorts. If heterogeneity was not found, the transformed yearly data were pooled, that is, the year designation was ignored, and steps 2-4 above were repeated on the pooled data.

An initial inspection of the blue marlin length-frequency distributions revealed some unusually large specimens identified as males weighing up to 328 kg, whereas it had been contended that male blue marlin in the Atlantic (Erdman 1968) and in the Pacific (Strasburg 1970) do not exceed about 136 kg. An examination of data collected under ideal sampling conditions at Hawaiian International Billfish Tournaments revealed only 5 out of 385 individuals in 12 yr that exceeded 136 kg. Four of these were under 143 kg while one fish weighed 171 kg. On the basis of these data, we accepted Erdman's and Strasburg's contention as essentially correct, assumed that all males over 143 kg were misidentified due to the difficult sampling conditions at the auction sites, and reclassified all males over 143 kg as females (56 were reclassified out of 2,710 specimens originally classified as males).

Transformation of Data

Observed weights were converted from pounds to kilograms and then to fork lengths in centimeters (tip of bill to middle point on the posterior margin of the middle caudal rays, FL). Length-weight relationships used for the latter conversions were calculated as functional regressions from Skillman and Yong (1974) following the recommendations of Ricker (1973). Briefly, the differences between functional and the commonly used predictive (linear) regressions, which are of importance to this application, are as follows. First, the predictive regression applies where it is hypothesized that one variable is linearly related to or dependent on a second variable, the independent variable. Whereas, the functional regression applies where it is hypothesized that two variables are interdependent, and the effect of one cannot be disentangled from the effect of the other. Second, the predictive regression tends to systematically underestimate the magnitude of the regression coefficient as the sample range truncates the real range of the variates; the functional regression does not do so. For striped marlin, the data were insufficient to calculate functional length-weight relationships for each sex; therefore, a single relationship ($FL = 73.4429\, W^{0.2858}$) was applied to each sex separately. For blue marlin, separate functional length-weight relationships were calculated ($FL_{\mathrm{FEMALE}} = 65.4502\, W^{0.3030}$, and $FL_{\mathrm{MALE}} = 56.8780\, W^{0.3318}$). As expected, the coefficients of allometry calculated using functional regressions increased over those calculated in Skillman and Yong (1974) using predictive regressions, and the difference between sexes decreased by 36%.

In order to efficiently separate age-groups from the frequency distributions, the data were grouped and length intervals set up (Simpson et al. 1960). Lengths for striped marlin were grouped by sex, year, quarter, and 3-cm interval, and these groupings resulted in a maximum of 96-length intervals per quarter. Blue marlin lengths were grouped by sex, quarter, year, and 5-cm interval, and these groupings resulted in a maximum of 73-size intervals per quarter.

Separation of Age-Groups

The computer program ENORMSEP (Yong and Skillman 1975) was used to separate the grouped, length-frequency data into constituent age-groups and to calculate estimates of the mean length, variance, percent representation, and numerical size of the age-groups. Essentially this computer program automates the Cassie-Harding probability paper method (Harding 1949; Cassie 1954) and enters intermediate results into NORMSEP which performs the actual separation of age-groups.

Progression of Age-Groups

The estimates of mean lengths for age-groups were plotted by quarter in order to check for reasonable progression and to assign age. Ages were assigned by determining the time of peak spawning, estimating the age at recruitment, and then merely assigning ages progressively as the age-groups passed through the fishery.

The time of spawning is not well established for either striped or blue marlin. For striped marlin, Nakamura (1949) stated that the time of peak spawning seemed to be from April to May in the South China Sea near the Republic of China and from May to June near the Bonin Islands. Royce (1957) stated that testes with free flowing milt were collected in the equatorial central Pacific in March. Kume and Joseph (1969) estimated, on the basis of gonad index of females taken in the eastern tropical North Pacific, that peak spawning occurs in May and June. From specimens landed in southern California and northern Mexico, Eldridge and Wares (1974) indicated that gonad index was highest in June and July, but they did not have samples for August or September. Hence, we took June 1st as the time of peak spawning and assigned an age of 1.46 yr to the 151-cm male and 152-cm female age-groups recruited in the fourth quarter.

For blue marlin, Royce (1957) stated that males with free flowing milt were collected from February through October in the equatorial Pacific, and cited Nakamura (1942) as indicating that spawning occurs east of Luzon (Philippines) from May to July. Kume and Joseph (1969), on the basis of gonad index of females taken in the eastern tropical Pacific, concluded that spawning occurs in December and January; however, most of their samples were collected from south of the equator. We arbitrarily took June 1st as the time of peak spawning and assigned an age of 0.71 yr to the 55.5-cm female age-group recruited in the first quarter.

Von Bertalanffy Growth Model

Two computer programs, BGC3 and BGC4, assembled by Abramson (1971) and written by Patrick Tomlinson were used in this paper to obtain estimates of von Bertalanffy growth parameters. The computer program for model 1, BGC3, fits the von Bertalanffy model by the least squares method to lengths from fish of known or, in this case, assumed age. The basic model is the familiar equation

$$L_t = L_\infty (1 - e^{-K(t - t_0)}) \qquad (1)$$

where L_t = length at age t

L_∞ = a parameter depicting asymptotic maximum length

K = a parameter indicating the rate of proportional growth

t_0 = a parameter depicting the theoretical age at which the fish has zero length given the adult growth form.

The computer program for model 2, BGC4, a version of the size-increment method proposed by Fabens (1965), fits the von Bertalanffy model by the least squares method to observed lengths, using data on growth increment in known time intervals but making no assumptions about absolute age. Parameter estimates using this method are included in the tables so that any future estimates of striped or blue marlin growth from tagging data can be compared directly to our results. For model 2, the von Bertalanffy model is written as

$$L_t = L_\infty(1 - be^{-Kt}) \qquad (2a)$$

where $b = 1 - \frac{L_0}{L_\infty}$ = a parameter depicting the theoretical proportion of potential growth in length that occurs after hatching;

or by substituting $t = t + \triangle t$ and $be^{-Kt} = 1 - \frac{L_t}{L_\infty}$ into Equation (2a)

$$L_{t + \Delta t} = L_t\, e^{-K\Delta t} + L_\infty (1 - e^{-K\Delta t}) \qquad (2b)$$

where $\triangle t$ = time increment between points of measured length.

GROWTH OF STRIPED MARLIN

Results—Analysis of Cohorts

Age-groups were successfully separated by sex and by quarter, within years, using the computer program ENORMSEP (Table 1). In general, the mean length estimates for females were slightly larger than those for males of the same age-groups. Quantitatively, the goodness of fit of the separated age-groups to the observed frequency distribution can be assessed with the chi-square values in Table 1. The largeness of the chi-square values indicated poor fit, but it was found that the tails of the distribution, having frequencies too small for the separation of age-groups, contributed disproportionately to the total chi-square value. Qualitatively, the goodness of fit was deemed adequate for the following reasons. In all years there was close agreement between sexes in the number of age-groups separated within quarters: approximately 2, 3, 4, and 3 age-groups for the first through fourth quarters, respectively. There was also close agreement among years and between sexes in the mean lengths and length composition of age-groups within quarters.

The progressions of mean lengths were set up as depicted by the connected open circles in Figure 1. In the third quarter of every year for both sexes, there was an age-group with mean length of about 167 cm that did not fit into the progression of age-groups. By assigning the same assumed age to this age-group as to a similar size group in the first quarter, and allowing the same time between spawning and the attainment of this age, this age-group could have resulted from a spawning in January. On the basis of gonad indices, Kume and Joseph (1969) believed that striped marlin from the eastern South Pacific spawn from November to December, and Royce (1957) indicated that striped marlin with ripe gonads have been collected in February in the equatorial region of the central Pacific. Hence, we concluded that this age-group belonged to a different spawning stock and should not be used in the calculation of the von Bertalanffy growth curves for the central North Pacific stock. Also, for females there were two age-groups having mean lengths of 267.5 and 200.0 cm in the third quarter 1964 and 1966, and for males there were four age-groups having mean lengths of 204.6 and 272.0 cm in the third quarter of 1968, 271.8 cm in the fourth quarter 1968, and 266.0 cm in the second quarter 1969. These could not be assigned with certainty to any cohort.

Several qualitative aspects of the observed growth of the cohorts were noteworthy (Figure 1). First, there seemed to be a cyclical pattern in the mean size at recruitment but no upward or downward trend. Second, the progression of age-groups during the first year in the fishery was fairly smooth and consistent between cohorts. Third, after about a year and a half in the fishery, there seemed to be a regression or slowing down in the apparent growth that persisted for two or three quarters. Fourth, the mean length of the last age-group in each cohort varied considerably.

There were a sufficient number of age-groups for the 1959-65 cohorts to fit a von Bertalanffy growth curve but not for the 1957-58 and 1966-68 cohorts. The calculated growth curves were shown as smooth curves in Figure 1. As expected from the variation shown in the progression of the observed mean sizes in Figure 1, the standard errors of estimates were moderate, and there was variation in parameter estimates between cohorts (Table 2).

To investigate the variation in estimates of mean length for age-groups shown in Table 1 and in growth parameters shown in Table 2, a series of nonparametric Friedman two-way analyses of variance was performed. No difference in the number of age-groups by sex, quarter, or sample year could be demonstrated (all S test statistics were insignificant with probability $P>0.05$, Hollander and Wolfe 1973:139). In testing the effect of sex on the mean length of age-groups within quarters, three significant effects ($S=5.44$, $P\leq 0.05$; $S=8.99$, $P\leq 0.01$; and $S=5.44$, $P\leq 0.05$) were found out of 16 comparisons. However, using a sign test for trends in mean length between sexes showed that females tended to be larger than males (test statistic P = 0.00005, or probability $P\leq 0.01$, for data from all years). In

TABLE 1.–Estimates of striped marlin age-groups (numbers do not indicate age) by sex and by year and quarter of sampling. Estimates of mean fork length, $\overline{FL}$; percent of total sample comprising a particular age-group, %; and chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

			Age-group 1		Age-group 2		Age-group 3		Age-group 4		Age-group 5		
Year	Quarter	Sex	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	χ^2
1960	4	M	150.9	3.4	205.7	86.6	220.8	10.0	—	—	—	—	64.2
		F	154.0	3.4	208.2	85.5	228.7	11.1	—	—	—	—	44.7
1961	1	M	160.2	50.4	208.7	49.6	—	—	—	—	—	—	16.4
		F	162.2	65.2	213.5	34.8	—	—	—	—	—	—	32.1
	2	M	176.5	27.5	215.7	72.5	—	—	—	—	—	—	70.6
		F	172.5	26.2	223.5	56.0	231.1	17.8	—	—	—	—	39.6
	3	M	161.1	18.7	184.7	26.9	203.3	14.8	223.6	39.6	—	—	20.8
		F	159.3	39.4	197.4	17.6	224.2	31.6	247.4	11.4	—	—	35.1
	4	M	156.7	11.2	207.8	72.8	220.6	16.0	—	—	—	—	8.6
		F	158.0	13.4	211.1	71.8	225.8	14.8	—	—	—	—	28.0
1962	1	M	175.8	49.4	211.9	50.6	—	—	—	—	—	—	18.7
		F	170.6	45.9	213.7	54.1	—	—	—	—	—	—	32.5
	2	M	181.7	15.9	215.2	81.0	238.4	3.1	—	—	—	—	47.7
		F	175.9	17.6	217.9	40.4	232.3	42.0	—	—	—	—	28.5
	3	M	169.0	28.7	191.4	37.1	213.4	30.7	225.0	3.5	—	—	24.8
		F	170.3	39.9	193.5	41.5	212.6	18.6	—	—	—	—	24.2
	4	M	149.7	45.4	209.1	49.4	218.8	5.2	—	—	—	—	79.5
		F	150.2	47.1	209.6	48.4	241.1	4.5	—	—	—	—	67.3
1963	1	M	162.9	76.6	210.3	23.4	—	—	—	—	—	—	61.9
		F	163.1	80.2	210.7	19.8	—	—	—	—	—	—	47.1
	2	M	173.9	35.4	217.8	62.8	230.7	1.8	—	—	—	—	66.2
		F	168.4	32.9	225.4	33.4	228.8	33.7	—	—	—	—	61.8
	3	M	171.0	3.4	187.2	19.9	217.4	76.7	—	—	—	—	10.8
		F	173.0	9.0	194.8	33.0	219.9	21.0	239.5	37.0	—	—	12.4
	4	M	151.0	14.7	202.0	59.0	216.5	26.3	—	—	—	—	32.0
		F	153.4	24.3	206.2	53.5	219.0	22.2	—	—	—	—	58.6
1964	1	M	173.5	76.7	206.3	23.3	—	—	—	—	—	—	77.4
		F	173.7	69.3	198.7	30.7	—	—	—	—	—	—	97.4
	2	M	186.3	38.8	209.7	52.8	227.3	8.4	—	—	—	—	63.2
		F	179.5	35.5	216.9	56.0	242.1	8.5	—	—	—	—	35.6
	3	M	164.3	26.0	191.3	21.3	205.3	49.1	228.7	3.6	—	—	15.3
		F	168.8	48.7	192.3	10.3	215.2	39.4	267.5	1.6	—	—	43.6
	4	M	160.7	1.9	203.5	94.2	217.2	3.9	—	—	—	—	99.8
		F	158.6	0.8	206.0	91.5	222.2	7.7	—	—	—	—	137.1
1965	1	M	159.8	3.2	203.2	96.8	—	—	—	—	—	—	49.3
		F	164.1	4.7	206.8	95.3	—	—	—	—	—	—	44.6
	2	M	172.7	7.5	212.5	90.9	232.4	1.6	—	—	—	—	34.3
		F	171.4	11.5	220.3	84.7	235.0	3.8	—	—	—	—	22.0
	3	M	164.6	27.0	193.8	18.3	211.7	40.2	230.6	14.5	—	—	6.7
		F	164.3	29.8	206.1	40.4	224.0	28.0	248.0	1.8	—	—	26.4
	4	M	144.5	3.0	205.9	88.5	225.5	8.6	—	—	—	—	47.3
		F	148.4	4.4	207.9	83.9	222.8	11.7	—	—	—	—	117.9
1966	1	M	158.6	14.3	207.7	85.7	—	—	—	—	—	—	37.0
		F	165.1	18.2	212.1	79.0	250.5	2.8	—	—	—	—	30.0
	2	M	182.3	23.6	215.5	76.0	249.6	0.4	—	—	—	—	32.1
		F	177.7	25.7	220.8	64.8	244.0	9.5	—	—	—	—	26.4
	3	M	171.3	17.0	198.6	69.2	218.6	10.8	234.6	3.0	—	—	15.5
		F	193.8	74.2	200.0	16.5	209.8	2.8	240.8	6.5	—	—	21.1
	4	M	147.9	3.4	206.5	94.0	236.3	2.6	—	—	—	—	142.0
		F	131.0	3.6	208.8	84.0	214.6	12.4	—	—	—	—	52.4
1967	1	M	159.4	6.2	204.3	93.8	—	—	—	—	—	—	44.8
		F	165.7	4.3	207.8	95.7	—	—	—	—	—	—	40.1
	2	M	171.9	1.5	208.2	97.8	233.0	0.7	—	—	—	—	24.8
		F	174.1	5.5	221.4	87.3	249.1	7.2	—	—	—	—	60.2
	3	M	168.3	27.7	192.8	53.7	213.4	3.5	232.5	15.1	—	—	10.5
		F	166.9	30.1	185.1	25.6	204.5	44.3	—	—	—	—	9.8
	4	M	168.7	0.7	202.7	93.4	218.9	5.9	—	—	—	—	82.9
		F	162.8	0.4	202.8	97.4	225.8	2.2	—	—	—	—	98.4
1968	1	M	161.7	1.6	200.7	98.4	—	—	—	—	—	—	37.6
		F	165.6	3.1	202.3	94.8	242.6	2.1	—	—	—	—	48.4
	2	M	174.6	2.2	208.1	97.5	242.0	0.3	—	—	—	—	58.1
		F	182.0	2.3	215.8	97.3	222.7	2.4	—	—	—	—	45.6
	3	M	169.0	9.4	194.7	63.7	217.1	16.0	204.6	6.7	272.0	4.2	30.9
		F	164.5	9.5	193.8	63.6	213.4	19.5	235.1	7.4	—	—	18.4
	4	M	157.7	5.3	205.5	93.9	271.8	0.7	—	—	—	—	79.4
		F	153.9	8.0	209.4	89.3	242.5	2.7	—	—	—	—	66.4

Table 1.—Continued.

Year	Quarter	Sex	Age-group 1		Age-group 2		Age-group 3		Age-group 4		Age-group 5		X^2
			$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	$\overline{FL}$	%	
1969	1	M	157.8	8.9	203.5	91.1	—	—	—	—	—	—	31.1
		F	156.6	12.6	206.6	87.4	—	—	—	—	—	—	32.2
	2	M	179.0	9.1	211.8	90.6	266.0	0.3	—	—	—	—	34.1
		F	182.0	0.4	212.0	97.0	221.9	2.6	—	—	—	—	39.4
	3	M	161.0	0.5	195.4	62.2	220.0	25.2	235.9	12.1	—	—	15.5
		F	174.7	8.3	196.8	71.2	221.0	13.8	241.4	6.7	—	—	40.2
	4	M	154.5	5.8	206.6	92.5	233.0	1.7	—	—	—	—	33.9
		F	155.3	4.8	206.0	93.4	236.2	1.8	—	—	—	—	70.9
1970	1	M	164.1	45.3	210.4	54.7	—	—	—	—	—	—	28.2
		F	164.2	47.4	208.2	52.6	—	—	—	—	—	—	35.9

testing significance of differences between the growth parameters, the analysis of variance failed to demonstrate an effect of either cohort or sex on L_∞, K, or t_0 (all S values insignificant with P>0.05). We concluded that there were no significant effects of either cohort or sex on the number of age-groups or growth parameters, and that females tended to be statistically larger at successive ages even though the magnitude of the differences was not significant.

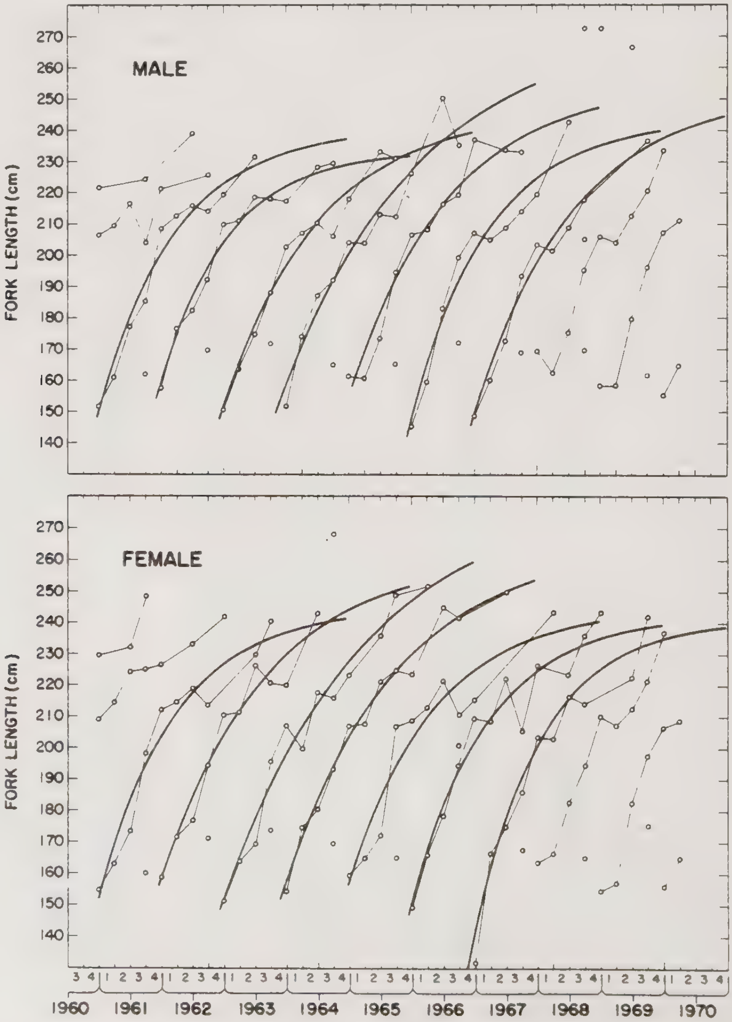

FIGURE 1.–Striped marlin von Bertalanffy growth curves (heavy lines) by sex for the 1959-65 cohorts. Observed mean lengths for age-groups, represented by circles connected with light lines, were used in fitting the growth curves.

TABLE 2.–Striped marlin von Bertalanffy growth parameters by cohort and sex. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the fish would have zero length), are given for model 1 (upper row) and model 2 (lower row).

Year-class	Sex	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
1959	Male	241.0	0.812	0.297	5.1
		251.1	0.651		6.1
	Female	245.0	0.809	0.294	6.6
		255.1	0.626		7.3
1960	Male	233.7	0.929	0.260	3.6
		233.5	0.986		4.7
	Female	261.7	0.584	−0.096	6.0
		290.0	0.437		8.0
1961	Male	247.0	0.640	0.007	4.6
		250.9	0.630		5.3
	Female	283.3	0.428	−0.304	6.0
		265.7	0.574		8.6
1962	Male	274.4	0.448	−0.435	6.8
		248.2	0.873		9.0
	Female	265.7	0.554	−0.125	3.7
		261.9	0.664		6.0
1963	Male	256.0	0.622	−0.004	6.2
		244.2	0.655		7.9
	Female	245.5	0.729	0.091	9.1
		258.7	0.607		10.9
1964	Male	243.7	0.818	0.351	7.1
		275.5	0.570		6.7
	Female	243.3	0.803	0.282	7.0
		234.9	1.067		9.8
1965	Male	253.3	0.630	0.086	4.3
		258.1	0.585		5.3
	Female	239.8	0.914	0.542	6.5
		231.5	1.267		8.9

Results—Analysis of Pooled Data

In the preceding section, it was shown that there were no demonstrable differences in the growth parameters between different cohorts; hence, the estimates for L_∞, K, and t_0 could be averaged to provide a pooled estimate. In addition, it was not possible to consistently show significant differences between quarters or years in the number of age-groups separated ($S=11.78$, $P>0.05$), the mean lengths of age-groups ($S=15.51$, $P\leq0.05$, for males in third quarter, all seven remaining S values had $P>0.05$), or the percent representation of age-groups ($S=57.18$, $P\leq0.01$, for males in the second quarter, $S = 49.57$, $P \leq 0.01$, for females in the third quarter, all six remaining S values with $P>0.05$). Neither was it possible to show a trend in mean lengths among cohorts using a series of sample runs tests (one test out of 18 deviated from random at the 0.05 level). We interpreted these results to mean that the yearly samples were homogeneous and that at least approximately a steady state existed. Therefore, the yearly frequency data were pooled; and ENORMSEP was used to separate age-groups.

The mean lengths and percent representation of age-groups by quarter (Table 3) were quite similar to the values found using the yearly data (Table 1). Quantitatively evaluating the goodness of fit, the chi-square values were found again to be rather large. Qualitatively, however, the shape of the frequency distributions was consistent between sexes within quarters and generally so between quarters within each sex (Figure 2). The plots for the third quarter, the off-season for striped marlin in Hawaii, did not show much of a pattern at all. Also, the shapes of the plots for the pooled data analysis were similar to those for the analysis of individual cohorts (not shown).

Mean lengths for females and males exhibited a fairly smooth progression (Figure 3). As in the analysis of cohorts, there was an age-group with mean length of about 167 cm in the third quarter that did not fit into the progression of age-groups. Again, it was assumed that this age-group belonged to a different spawning stock and should not be used in the calculation of the growth curve. For females, there were 11 age-groups in the progression whereas there were 10 or 12 but never 11 for the analysis of cohorts. For males, there were 12 age-groups in the progression whereas there were 9 to 11 in the analysis of cohorts. The smallest fish were recruited into the fishery in the fourth quarter and progressed through the fishery until the largest fish passed from it in the third

TABLE 3.–Statistics for striped marlin age-groups by quarter and sex, pooled over all years. Estimates of mean fork length, $\overline{FL}$; percent representation of the age-group, %; the numerical sample for size of the age-group, n; the total sample size, N; and the chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

Quarter	Age-group	Male			Female		
		$\overline{FL}$	%	n	$\overline{FL}$	%	n
1	1	166.6	36.2	1,480	167.1	42.6	1,568
	2	204.7	63.8	2,613	207.2	57.4	2,115
	N			4,093			3,683
	χ^2	114.1			183.8		
2	1	177.3	17.5	1,020	174.4	21.0	852
	2	212.5	81.5	4,746	219.7	69.7	2,827
	3	228.0	1.0	57	238.4	9.3	377
	N			5,823			4,056
	χ^2	97.2			54.0		
3	1	167.1	17.0	178	166.7	22.7	190
	2	195.3	52.6	551	194.0	50.1	419
	3	215.2	19.9	208	217.5	19.4	162
	4	231.6	9.1	96	236.2	7.8	65
	5	260.0	1.4	14	—	—	—
	N			1,047			836
	χ^2	71.6			45.1		
4	1	151.3	7.1	421	152.2	8.7	431
	2	204.7	87.0	5,162	207.0	83.0	4,113
	3	222.6	5.9	352	222.7	8.3	413
	N			5,935			4,957
	χ^2	130.1			192.3		

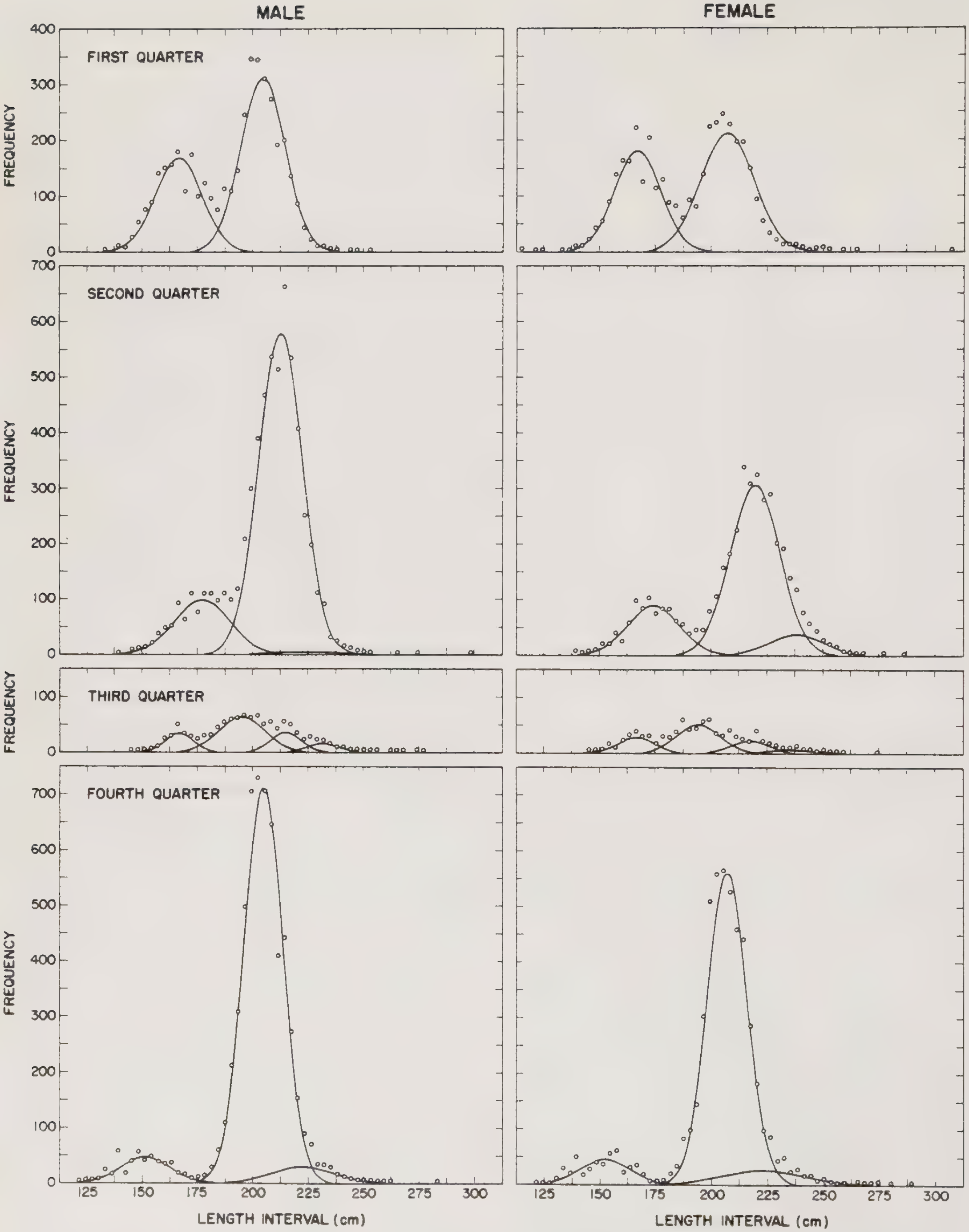

FIGURE 2.–Striped marlin length composition by sex and quarter for the analysis of pooled data. The smooth curves represent age-groups separated by the computer program ENORMSEP, and circles represent observed values.

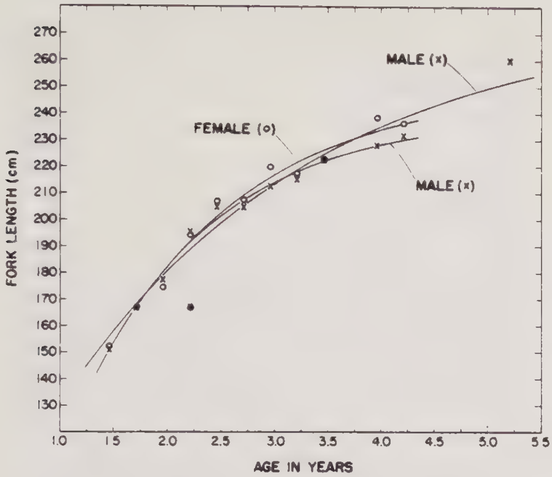

FIGURE 3.–Striped marlin von Bertalanffy growth curves by sex, for the analysis of pooled data. Male and female growth curves having the same length were obtained using 11 age-groups while the longer male curve was obtained using in addition an age-group 1 yr older. Observed mean lengths for male and female age-groups are given. As explained in the text, the outliers at age 2.46 yr were not used in fitting the growth curves.

quarter 3 yr later for females and 4 yr later for males.

Discussion

We felt that the parameter estimates from the analysis of pooled data provided better estimates of population parameters than those from the analysis of individual cohorts because pooling smooths out variation in individual curves. In addition, the less well-represented age-groups, having small and large mean lengths and being recruited to or escaping from the fishery, were estimated more accurately given the larger sample size after pooling.

Since estimates of mean lengths at age were used in the fitting of the growth curves, estimates of growth parameters are in terms of these average values. Likewise, estimates of length at age derived from these models (Table 4) will actually be average values and should only be calculated for the range of ages used in fitting the models. In fact, the greatest utility of these models will be to predict length at ages within the range of the observed data. The accuracy of the estimation of L_∞ is dependent on the range of values used, and it should be remembered that the data used here included fish only up to the onset of sexual maturity.

TABLE 4.–Striped marlin von Bertalanffy growth parameters by sex for analysis of pooled data. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the marlin would have zero length) are given for model 1 (upper row) and model 2(lower row).

Sex	Case	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
Male	All age-groups	277.4	0.417	−0.521	5.5
		314.4	0.315		5.5
Male	Less oldest age-group	239.7	0.810	0.235	2.8
		240.0	0.809		3.7
Female	All age-groups	251.0	0.696	0.136	4.2
		251.8	0.709		6.2

The estimation of population L_∞ was complicated by the fact that males and females were not represented in the fishery for the same length of time. Obviously, the length of time (number of age-groups) that the sexes were in the fishery had an effect on the estimation of L_∞, as well as K and t_0 (Table 4). We believed that the parameter estimates for males using all 12 age-groups provided the most accurate estimates because a greater part of the growth curve was measured. We must admit that the estimates may not be very precise because the estimated sample size of the last age-group was 14 individuals, and the standard error of the estimate for the growth curve was larger when all age-groups were included. The estimates of L_∞ for males using models 1 and 2 were 277.4 and 314.4 cm, respectively. In order to obtain estimates for females that can be compared to those for males, the differences found between females and males using 11 age-groups, 11.3 and 11.8 cm for models 1 and 2, respectively, were added to the estimates of L_∞ for males, giving 288.7 and 326.2 cm, respectively. These estimates seemed reasonable when compared to the largest striped marlin measured by personnel from the Honolulu Laboratory: 296 cm for males, 305 cm for females, and 310 cm for sex undetermined.

Both the analysis of cohorts and the pooled data analysis (though less so) were plagued by apparent negative growth or at least by very slow growth during some quarters about a year and a half after recruitment. Accepting the general growth progression as valid, this problem probably biased the estimates of L_∞ downward and K upward and contributed to the size of the standard errors of estimates. We do not believe that this period of apparent negative growth resulted from some physiological change in the form of growth for which the von Bertalanffy model could not account and, therefore, is invalid, but rather that the apparent change in growth was caused by seasonal changes in availability of the stock due to some seasonal size-age migration phenomenon or possibly by changes in the selectivity of the fishery. Preliminary examination of Japanese longline statistics suggested that the striped marlin stock available to the Hawaiian fishery shifts its center of density northward in the months with the warmest water temperature and becomes less available to the local fishery (Heeny S. H. Yuen, Southwest Fisheries Center, pers. commun.). The decreased growth most commonly seen in the third quarter might then be due to smaller fish being associated with the periphery of the stock.

There are of course other possible explanations. For example, one reviewer suggested that this period of slow or negative growth represented an asymptote followed by the initiation of a new growth phase. Fitting a two-cycle Gompertz growth curve to the pooled data, this reviewer found both sexes tending toward an asymptote at age 2.46 yr followed by another growth phase where females tended toward an asymptote at 320 cm, but no solution was found for males. Such changes in growth phase are common at sexual maturity and at other times when body form changes. Change in growth form is commonly accompanied by a corresponding change in the length-weight relationship, and Skillman and Yong (1974) found no indication of a change in the length-weight relationship over the range 142.2-310.1 cm. Also, the age of fish in the Hawaiian fishery, having a calculated mean length corresponding to length at first maturity found by Eldridge and Wares (1974) and Kume and Joseph (1969) for the eastern tropical Pacific, was 4.2 yr. This age is nearly double the hypothesized age of first asymptotic growth. Thus, while it is possible to fit a segmented growth curve to the data, biological evidence given above does not support such a procedure.

Another possible explanation involves the separation of age-groups. The aberrant growth occurred most frequently in the third quarter, and since the sample size was smallest in this quarter, the precision of the estimates is probably less than for the other quarters. However, the aberrant growth did not always occur in this quarter, and its repeated occurrence among cohorts suggested that it was real and not an artifact of the estimation procedure per se. With any probabilistic means of separating age-groups from a mixed distribution, there is always the danger that age-groups from different cohorts of the same spawning stock will be so similar in size that they cannot be separated, especially with increasing age and varying growth rates of the cohorts. We acknowledge that this may be a problem, but if it is, it would seem from Figure 1 to be more important for the growth period following the period of aberrant growth. This problem would be increased if there were more than one spawning stock involved, and this seems to be the case for some quarters. In spite of the small sample sizes in the third quarter, there seemed to be little doubt that the 167-cm age-group was real, since its mean length is quite removed from that of the next age-group at about 194 cm and since the age-group was found for the pooled data analysis and for 8 out of 9 yr for females and for all years for males in the analysis of yearly data. Because the two spawning stocks would continue to have quite different lengths for the next couple of quarters and no comparable age-groups were separated in these quarters, it was reasonable to assume that this other secondary stock was not represented in the catches in the subsequent fourth, first, and probably second quarters. But what about the following third quarters? If similar growth curves are assumed for this other stock, then the 200.0-cm female age-group in the third quarter of 1966 and the 204.6-cm male age-group in the third quarter of 1968 could also belong to the secondary spawning stock. If this secondary stock was present in other years but in numbers too small to be separated out, it would tend to bias downward the estimates of the similar-sized age-group of the primary spawning stock. With the accuracy of the present set of data, it is impossible to comment on the likelihood or importance of this possibility.

The occurrence of these age-groups at approximately 167 cm in the third quarter presents an additional problem. Where do they come from? If the male and female growth curves are used to back calculate the probable time of spawning for the age-group at approximately 167 cm in the pooled data analysis, January is estimated as the time of peak spawning. We hypothesize that these fish could come from a stock spawning in the equatorial region, probably north of the equator, during months corresponding to the southern summer. It is hard to visualize a hypothesis that would account for a stock spawned 6 mo out of phase migrating poleward, but at lower latitudes, at the same time as the primary stock. Possibly these fish associate with blue marlin of about the same size that migrate into Hawaiian waters in the third quarter.

Estimates of von Bertalanffy growth parameters for both sexes were first obtained using for females and using 12 and 11 (deleting oldest) age-groups for males (Table 4, smooth curves in Figure 3). The standard errors of estimates were slightly smaller than those for the individual cohorts but still not what could be considered small. When the oldest age-group for males was deleted from the calculations, L_∞ for females was 11 to 12 cm greater than for males. Using all of the age-groups for males, the estimate of L_∞ increased substantially.

Although this paper deals with growth, the length composition and age of striped marlin as found in this study have some relevancy to the problem of migration. First, Matsumoto and Kazama (1974) hypothesized that striped marlin migrate out of Hawaiian waters to spawn, most likely to the western North Pacific. The calculated mean length of the last female age-group found in the Hawaiian fishery (age 4.2 yr) corresponded to the length at first maturity found by Eldridge and Wares (1974) and Kume and Joseph (1969) for the eastern tropical North Pacific. Thus, our data established that as striped marlin reached the length corresponding to sexual maturity, they became unavailable to the local fishery. Second, Kume and Joseph (1969) indicated that there was a tendency for average length to increase in the southern areas of the Japanese longline fishery in the eastern tropical North Pacific, and it seemed to us from their charts that there was also a western component to the increasing average lengths. Eldridge and Wares (1974) believed that maturing striped marlin moved out of the range of the sport fisheries based in southern California and Mexico; and Squire (1974) suggested that the movement of striped marlin away from the Baja California area might be to the area of the Revilla Gigedo Islands where fish with ripe gonads have been collected and where behavior suggestive of spawning activity has been observed by the Japanese. While the range of our length data was similar to that found in the eastern tropical Pacific, the last age-group recognizable in our data comprised less than 10% of the total frequency whereas similar-sized fish seemed to be well represented in the southern and western areas of the eastern tropical North Pacific longline fishery. Thus, it seems apparent that the fish leaving the fishery off the American coast do not migrate through the Hawaiian fishery in any appreciable numbers. However, the capture of a striped marlin, tagged off Baja California, 322 km southwest of the Hawaiian Islands indicates that some eastern Pacific fish move into the vicinity of the Hawaiian Islands. Finally, our analyses do not provide any information on the direction of emigration from the Hawaiian fishery.

GROWTH OF BLUE MARLIN

Results—Analysis of Pooled Data

The number of age-groups, as separated by the computer program ENORMSEP, varied from three in the third quarter for males to as many as eight in the first quarter for females (Table 5). The

TABLE 5.—Statistics for blue marlin age-groups by quarter and sex for analysis of pooled data. Estimates of mean fork length, $\overline{FL}$; percent representation of the age-group, %; the numerical sample size for the group, *n*; the total sample size, *N*; and the chi-square goodness of fit value, χ^2, were obtained from the computer program ENORMSEP.

		Male			Female		
Quarter	Age-group	$\overline{FL}$	%	*n*	$\overline{FL}$	%	*n*
1	1	123.0	3.3	2	55.5	0.6	1
	2	172.7	8.7	5	145.9	1.8	3
	3	225.0	57.2	34	190.5	3.0	5
	4	240.5	20.0	12	232.8	7.4	12
	5	281.8	10.8	7	286.8	31.5	52
	6	—	—	—	333.5	32.9	55
	7	—	—	—	366.1	22.2	37
	8	—	—	—	415.5	0.6	1
	N			60			166
	χ^2	16.8			33.2		
2	1	180.5	0.3	1	205.7	5.9	28
	2	220.0	65.4	172	298.3	76.2	365
	3	250.1	31.7	84	345.4	13.0	62
	4	278.0	2.6	7	377.2	4.9	24
	N			264			479
	χ^2	22.0			34.1		
3	1	163.6	1.4	9	158.8	0.4	3
	2	227.7	77.6	486	213.5	7.3	48
	3	255.8	21.0	131	292.6	53.1	352
	4	—	—	—	327.1	24.2	160
	5	—	—	—	362.9	15.0	100
	N			626			663
	χ^2	33.2			38.5		
4	1	175.5	8.4	32	101.7	0.9	4
	2	228.7	80.7	304	180.8	9.2	41
	3	264.0	10.4	39	225.1	11.3	51
	4	285.5	0.5	2	280.0	33.5	151
	5	—	—	—	307.6	14.2	64
	6	—	—	—	342.1	27.4	123
	7	—	—	—	390.8	3.5	16
	N			377			449
	χ^2	26.2			69.3		

shape of the frequency distribution differed substanially between sexes (Figure 4). The 240.5-cm male age-group separated in the first quarter that had zero variance (Table 5) was regarded as false and was not used in subsequent calculations. Quantitatively, the chi-square values do not indicate very good fit; however, as was the case with striped marlin, the tails of the frequency distributions, having frequencies too small for the separation of age-groups, contributed disproportionately to the total chi-square value. Qualitatively, as can be seen from Figure 4, the shape of the frequency distribution was similar from quarter to quarter, especially for males.

Progressions of mean lengths were set up for males and females as depicted in Figure 5. The smallest blue marlin recruited into the fishery in the first quarter were females, with males being recruited 1 yr later. Males were present in the fishery for 3¾ yr and females for 7 yr. Several age-groups represented by one or two individuals were separated for both sexes. The existence of these age-groups was tentatively accepted, but the accuracy of their estimated mean lengths was viewed with skepticism in calculating growth parameters. The mean length estimates of male and female age-groups were in close agreement until about 250 cm ($S = 0.50$, $P>0.05$). From 250 to 300 cm, the mean lengths for female age-groups were larger than estimates for males. Above 300 cm, only female age-groups were found, and these formed an irregularly increasing progression.

Estimates of von Bertalanffy growth parameters for both sexes were first obtained using

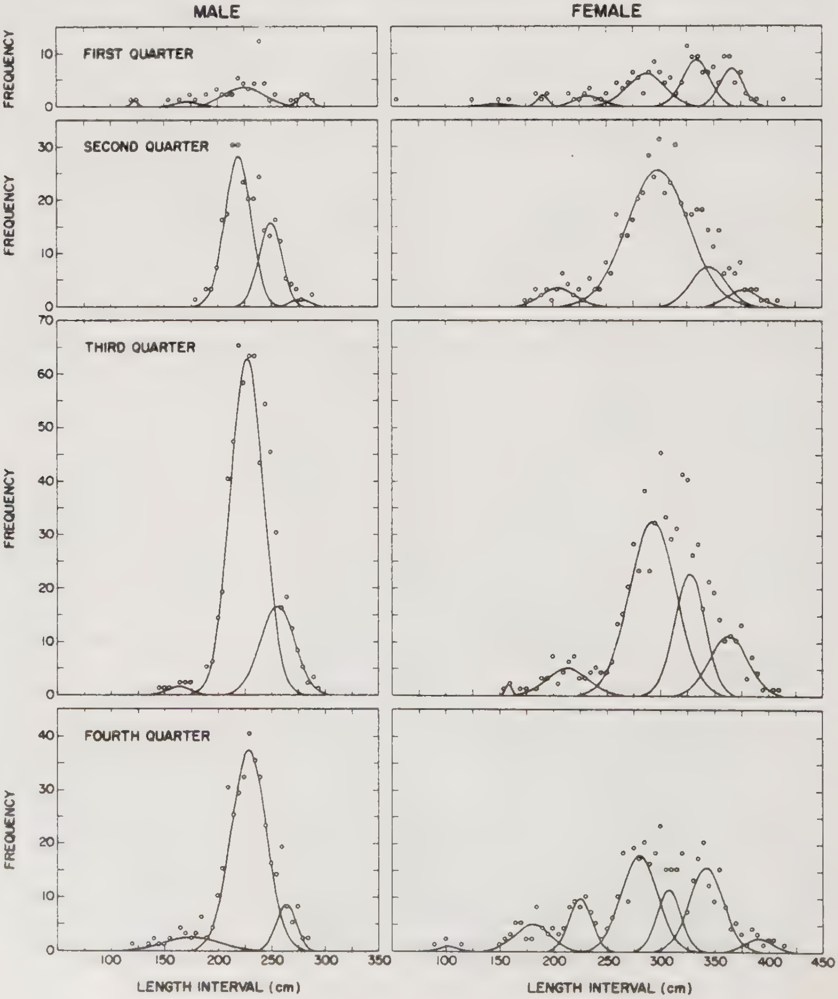

FIGURE 4—Blue marlin length composition by sex and quarter for the analysis of pooled data. The smooth curves represent age-groups separated by the computer program ENORMSEP, and circles represent observed values.

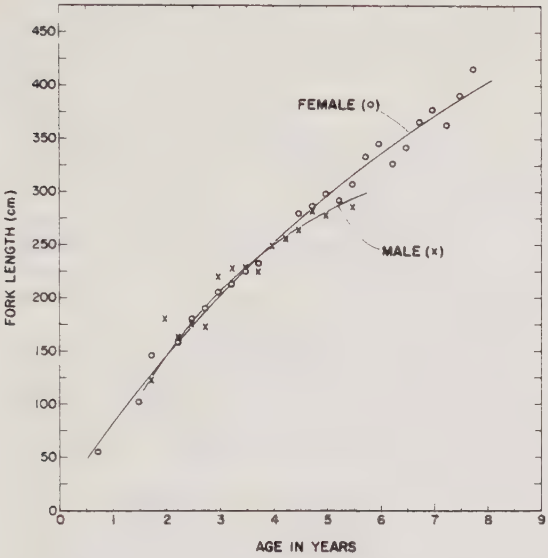

FIGURE 5.–Blue marlin von Bertalanffy growth curves by sex for the analysis of pooled data. Observed mean lengths for female and male age-groups are given.

all age-groups, and then using only those with estimated numerical representations greater than two individuals. Further analyses were done using age-groups for females, over the same age span as for males, with numerical representation greater than two individuals (Table 6). For males, parameter estimates were similar using all age-groups and those age-groups represented by more than two individuals. The standard error of estimate was smaller for the latter than it was for the case using all age-groups. For females, again the parameter estimates were similar for the two data sets, and the standard errors of estimates did not change appreciably. The estimates for L_∞ were nearly doubled those for males. In addition, the estimate of L_∞ for females, using the same age-groups as for males with age-groups represented by more than two individuals, was nearly 3½ times that for males.

TABLE 6.–Blue marlin von Bertalanffy growth parameters by sex for the analysis of pooled data. The parameter estimates, L_∞ (asymptotic maximum fork length), K (rate of proportional growth), and t_0 (theoretical time at which the fish would have zero length) are given for model 1 (upper row) and model 2 (lower row).

Sex	Case	L_∞ (cm)	K	t_0 (yr)	Standard error of estimate
Male	All age-groups	371.1 282.3	0.285 0.815	0.106	12.7 18.6
Male	Age-groups with more than two individuals	368.0 298.8	0.315 0.560	0.390	9.9 15.0
Female	All age-groups	659.1 807.8	0.116 0.091	−0.161	10.2 13.8
Female	Age-groups with more than two individuals	626.6 540.2	0.123 0.175	−0.202	9.1 14.0
Female	Same age-groups as for males with more than two individuals	1,248.1 875.2	0.048 0.086	−0.674	4.0 5.2

Discussion

The estimates of von Bertalanffy growth parameters for male blue marlin differed little whether all of the age-groups were used or whether the less well-represented age-groups were deleted (Table 6). Because the standard errors of estimates were generally smaller for the reduced data sets, we felt that these fits provided better estimates of parameters. Although the standard errors of estimates were larger than desirable, they varied from less than 1% to only 7% of the estimated L_∞. Thus, the von Bertalanffy growth model described the data satisfactorily. The mean length estimates for the poorly represented age-groups, which were the youngest and oldest in our samples, should be viewed as approximate.

For males, estimates of L_∞, 368.0 and 298.8 cm for models 1 and 2, respectively, bracketed the commonly accepted asymptotic length of about 300 cm. If our assumption of a knife-edge limit of 143 kg (approximately 300 cm) for males was incorrect, the progression of age-groups would have been expected to increase in length up to this point without approaching an asymptote. Since an asymptote was found, we felt our assumption was valid.

For females, the von Bertalanffy growth curves seemed adequate for describing the data, but the estimates of growth parameters were not biologically reasonable. Using the same range of age-groups as used for males, the estimates of L_∞ were around 1,000 cm, confirming the visual impression that there was little tendency towards an asymptote over this range of ages. Using all of the data, estimates of L_∞ were 626.6 and 540.2 cm for models 1 and 2, respectively, or approximately 1,729 and 1,060 kg, respectively. While these results suggested that there was some tendency towards an asymptote, which is not visually apparent in the data, we do not believe that enough older age-groups were included in the regressions to obtain valid estimates of L_∞ or K. Among fishery biologists, there seems to be less of a consensus on the maximum size of females than of males, but generally it is thought that female blue marlin have a maximum weight of less than 900 kg. Hence, our estimates of L_∞ seemed too large.

ACKNOWLEDGMENTS

The efforts of many people collecting data over a 10-yr period from the fresh fish auctions in Honolulu have made this paper possible. Thanks are extended to James B. Reynolds, Luis R. Rivas, Michael F. Tillman, and the anonymous reviewers for their helpful comments on an earlier version of this manuscript.

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7643

Temperature Discrimination by Captive Free-Swimming Tuna, *Euthynnus affinis*[1]

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ABSTRACT

Captive kawakawa, *Euthynnus affinis*, were instrumentally conditioned to respond to an increase in temperature to determine discrimination abilities. Two fish yielded a discrimination threshold of 0.10 to 0.15 C. Thermal sensitivity of this high-seas pelagic fish is thus no more acute than that of inshore fishes and appears inadequate for direct sensing of weak horizontal temperature gradients at sea.

Tunas (family Scombridae) are distributed within definite ranges of sea temperature (Thompson 1917; Clemens 1961; Broadhead and Barrett 1964) so consistently that fishery biologists use temperature to predict catches (Hester 1961; Johnson 1962). No one has clearly determined, however, whether temperature differences directly influence scombrid behavior. Precise sensing of temperature differences could be important or even essential for direct thermal mediation of tuna distribution. In order to estimate temperature discrimination thresholds, we developed and applied a method for use with these pelagic, continuously swimming fishes.

METHODS

Captive kawakawa, *Euthynnus affinis* (Cantor), 36 to 66 cm in fork length were held in circular pools 7.3 m in diameter and 1.2 m deep at the Kewalo Research Facility of the National Marine Fisheries Service, Honolulu, Hawaii; Nakamura (1972) described techniques for maintaining and handling live scombrids. Individual fish were then trained and tested in a similar pool over several months. Previous studies with unrestrained scombrids have estimated visual acuity (Nakamura 1968), auditory thresholds (Iversen 1967, 1969), and olfactory abilities (Van Weel 1952; Tester et al. 1953; Tester et al. 1955).

An instrumental conditioning technique was employed. Fish were trained to swim through an open trough in the tank (a "pass") during 5-min trial periods. Water flowed into the trough from above at about 6.5 liters/min (initiation of the water flow signaled the start of a trial). The temperature of this water flow (thermal stimulus) was ambient or heated. As the fish swam through the trough, it came in contact with this water flow. We used an ambient temperature stimulus (24 C) for half the trials and heated stimulus (40 C) for the other half. The 5-min trials, heated and ambient, were alternated in a quasi-random order (Gellermann 1933) and were separated by 5-min intertrial periods. If the stimulus was ambient, the fish would continue to make passes through the trough to receive

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Table 1.—*Last 12 days of data for fish K8 tested for temperature discrimination threshold (see Fig. 1 for graph of data). The number of passes made during each part of the trial-pair is given in chronological order. Each trial-pair consists of two subtrials (one heated and the other ambient). The number of passes made during ambient (reinforced) trials is given in boldface type. Lightface numbers represent incorrect passes made during heated trials. (It would be impossible to reduce this number to zero since the fish was required to make at least one pass each trial to contact the stimulus water flowing into the trough.) The last columns represent parameters used in the statistical test (*n = *number of pairs minus any pairs whose difference is zero.* T = *the smaller of the sums of the like signed ranks), and the temperature change encountered during heated trials for that particular day (C).*

	Trial-pair														
Day	1	2	3	4	5	6	7	8	9	10	11	12	*n*	*T*	C
1	32/20	19/19	23/15	16/39	23/17	27/20	32/12	37/13	23/34	28/17	16/33		10	0	1.00
2	27/18	26/20	25/15	25/33	26/21	13/36	41/10	29/25	24/10	26/10			10	0	0.50
3	35/18	23/13	22/6	15/7	18/13	15/15	7/11	14/5	26/15				8	1	0.30
4	36/12	36/7	15/29	10/12	8/33	29/4	37/9	24/12	29/15	15/18			10	1	0.20
5	38/27	28/12	33/19	19/28	22/38	29/30	24/16	25/11	13/12	19/4	14/32	22/18	12	6	0.20
6	23/10	20/7	7/11	31/5	12/24	19/11	25/13	10/31					8	1	0.15
7	27/24	18/19	14/8	22/22	10/20	15/15	14/23	13/7					6	1	0.10
8	29/15	16/11	8/14	20/13	28/23	29/22	14/15	19/13	16/7				9	1	0.15
9	25/30	16/17	8/14	19/7	12/8	13/12	15/17	11/14	12/13	12/17			10	30	0.10
10	14/8	12/5	9/7	15/13	8/10	9/3	4/5	18/15					8	0	0.15
11	21/16	18/13	15/17	20/10	17/14	17/12	16/19	13/16					8	7	0.10
12	14/11	8/8	7/6	17/8	7/9	8/8	5/9	11/6	14/12				7	0	0.15

food reinforcement; the food was pieces of thawed smelt (family Osmeridae). If the stimulus was heated, the fish would not receive any food reinforcement for passes. Most fish learned in 1 day to make more passes under ambient temperature conditions. The number of passes made during trials and intertrials was recorded for analysis; fish never made passes during intertrial periods. Each day, successive trials were paired for examination with a Wilcoxon matched-pairs, signed-ranks test (Siegel 1956)[3] (Table 1).

Work on threshold determination progressed over several months for each fish. A 90-sec variable interval schedule (Ferster and Skinner 1957) of reinforcement was introduced gradually to minimize reinforcement cueing. The temperature of the water stimulus during heated trials was also gradually decreased toward ambient. The temperature at the water flow directly encountered by the fish is of greatest importance and was measured with a 0.01 C graduated mercury thermometer. It is these measured and encountered temperature differences, rather than direct heat input to the system, that are used in the present analysis. If fish discriminated a given temperature difference, a smaller difference was presented at the next day's testing session. If fish did not distinguish between ambient and heated water, the temperature difference (heated minus ambient) was considered below threshold. Temperature threshold was defined as the midpoint between the smallest temperature difference fish discriminated and the greatest difference they did not discriminate.[4]

Initial experiments were conducted and recorded manually. The last fish was tested automatically: logic circuitry,[5] an underwater photosensor assembly in the trough, and a four-channel event recorder controlled the stimulus presentation, recorded and reinforced the fish's performance.

RESULTS

Two fish yielded temperature discrimination thresholds; six others jumped out of the tank during training and died. Results of the last 12 days of testing on the two fish provided threshold estimates of 0.10 C for the manually tested fish and 0.125 C for the automatically tested fish, the latter being our more reliable estimate (Fig. 1). To control for possible discrimination of extraneous stimuli [e.g.,

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[3] Our tests were run with $P = 0.01$ (for a one-tailed test).

[4] This is essentially the "staircase" technique used extensively in sensory threshold determination. The method is discussed in Dixon and Mood (1948) and Tavolga and Wodinsky (1963).

[5] Lehigh Valley Electronics Inc., Box 125, Fogelsville, Pennsylvania 18051. Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA, or the University of Wisconsin, Madison.

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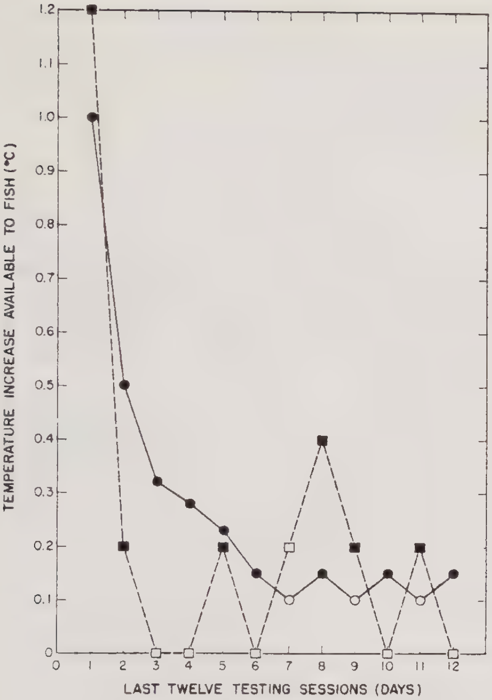

FIGURE 1.—*Discrimination ability of fish during last 12 days of testing for temperature thresholds. Squares represent fish K3 (1.45 kg, 45.6 cm fork length) tested manually. Threshold was determined as midway between 0.0 and 0.20 C (0.10 C). Circles represent fish K8 (2.39 kg, 50.0 cm fork length) tested automatically. Threshold was determined as midway between 0.10 and 0.15 C (0.125 C). For both fish, closed symbols represent days of significant thermal discrimination at* P $\leqslant$ *0.01; open symbols represent days of no apparent thermal discrimination at* P $\leqslant$ *0.01 (not even significant at* P $\leqslant$ *0.05).*

relay sounds, electric fields, reinforcement scheduling, etc. (Steffel 1973)], control systems were utilized periodically during the testing sessions. In one case, water was treated as in normal trials but heat added during heated trials was dissipated prior to delivery of the stimulus water to the tank. To do this, stimulus water was piped through a stainless steel coil over which cold water passed, reducing heated-stimulus-trial water to ambient temperature. Discrimination was not evident between ambient water and this water heated 1.0 C above ambient and cooled back to ambient. Therefore, fish in our experiments could only have been discriminating temperature differences and not nonthermal stimuli incidental to heated trials.

DISCUSSION

Many species of fish have been conditioned to respond to temperature differences of 0.03 to 0.25 C (Wells 1914; Bull 1936; Dijkgraaf 1940; Bardach and Bjorklund 1957). Most studies involved unrestrained fishes and positive reinforcement (food); however, all these previous experiments used small, benthic or inshore fishes and the techniques of classical conditioning. Our study is the first temperature-threshold determination utilizing larger, free-swimming pelagic fishes and instrumental conditioning methods. Previous work on restrained skipjack tuna, *Katsuwonus pelamis*,[6] using classical conditioning has indicated that scombrids could respond to temperature differences of 1 to 2 C (Dizon et al. 1974). While our current threshold values (0.10–0.15 C) fall within the range of published thresholds for other marine and freshwater fishes, they would apparently still preclude a scombrid from orienting to the gradual horizontal gradients of the ocean (0.0001–0.001 C/m). If temperature is indeed a primary factor controlling tuna distribution, a mechanism other than direct sensing of horizontal temperature differences is responsible, or our results are conservative estimates. Other work analyzing scombrid behavior in thermal gradients is in progress.

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[6] Sometimes still referred to as *Euthynnus pelamis* (Linnaeus). In any case, skipjack tuna are very closely related to the kawakawa and they are sometimes placed in the same genus.

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AGE AND GROWTH OF THE NEHU, *STOLEPHORUS PURPUREUS* (PISCES: ENGRAULIDAE), FROM THE HAWAIIAN ISLANDS AS INDICATED BY DAILY GROWTH INCREMENTS OF SAGITTAE

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ABSTRACT

Direct evidence is presented that the sagittae of nehu, *Stolephorus purpureus*, grow by discernible daily increments. Aging by daily growth increments provides the means to establish a general growth curve for the first 6 mo of life for this species. Adult nehu exhibit nearly linear growth between 30 and 60 mm standard length. Preliminary evidence is presented that the nehu population of Pearl Harbor may grow more rapidly than that of Kaneohe Bay.

Attempts to age tropical fishes by conventional methods have generally been thwarted by the absence of well-defined annuli in calcarious structures and protracted spawning periods which make length-frequency mode progression analyses difficult. Recognizing that exceptions to the above statement exist, Pannella's work (1971) providing indirect evidence of the presence of daily growth layers and periodical deposition patterns in the sagittae (otoliths) of three species of boreal fishes from the western North Atlantic suggested a means for conducting age and growth studies of tropical species. He concluded in that report: "Preliminary observation of growth patterns in sagittae of other species, living at various depths and different climates, appears to support the idea that daily growth may be a universal feature of fish otoliths." Pannella's (1974) later work in Puerto Rico provided circumstantial evidence of daily growth layers in sagittae of several species of tropical fishes.

To gain direct evidence that daily growth increments exist in tropical fishes we studied the nehu, *Stolephorus purpureus* Fowler, a small engraulid endemic to the Hawaiian Islands. The nehu is the basis of a live-bait fishery producing about 4,000 metric tons annually of skipjack tuna, *Katsuwonus pelamis* (Linnaeus), from the vicinity of the Hawaiian Islands. *Stolephorus purpureus* is a short-lived species (less than 1 yr) and has been the subject of relatively numerous studies: Nakamura (1970) has summarized the biological knowledge of this species available through 1965. Our work provides evidence of the presence of daily growth increments in the sagittae of nehu and permits the assembly of a growth curve for the first 6 mo of life for this species.

Brothers et al. (1976) have recently demonstrated the presence of daily growth increments in larval *Engraulis mordax* Girard and *Leuresthes tenuis* (Ayres) and presented evidence that the phenomenon occurs in several other species of California fishes.

METHODS AND MATERIALS

The nehu samples were taken with three types of gear in Pearl Harbor and the southeastern end of Kaneohe Bay, Oahu, Hawaiian Islands. Adults and juveniles (> about 30 mm standard length (SL)) were sampled with commercial bait seines (square mesh measuring 3.2 mm to a bar) in Pearl Harbor. Postlarvae (about ⩾ 20 mm SL), juveniles, and adults were obtained in Kaneohe Bay by a similar seine having a bar mesh measurement of 1.6 mm. Larvae (< 20 mm SL) were obtained near Coconut Island by personnel of the Hawaii Institute of Marine Biology with 0.5-m ring nets with mesh sizes of 550 μm.

Three separate holding experiments were conducted to test the hypothesis that the sagittae of nehu grow by discernible daily increments. All animals for these experiments were collected in Pearl Harbor and held in tanks of 38-kl capacity at the National Marine Fisheries Service (NMFS) Kewalo Basin Facility. The tanks were supplied with well seawater of 23°-24°C and 33-35‰ salinity at a rate of about 300 liters/min. The nehu

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were fed with frozen and live brine shrimp, *Artemia* sp., under variable regimes as described below. Each experimental population of nehu was sampled during placement in holding tanks, and then subsampled at various time intervals as described for each experiment. Otoliths were extracted from most specimens within a few hours of sampling. The remaining samples were frozen in seawater or preserved in 75% solution of isopropanol until extraction of otoliths (removal of tissue from otoliths of alcohol preserved specimens is difficult).

The first holding experiment was begun 5 April 1972. A 16-day sample (21 April) and a 34-day sample (9 May) were obtained from this population. The animals were fed once a day with frozen and/or live brine shrimp. The second holding experiment was begun 15 December 1972. This population was initially fed once a day. A high mortality was observed during the first 2 wk, after which food was provided twice daily. Samples were collected weekly after 1 mo of captivity. We examined sagittae from animals collected on 19 January and 26 January 1973. The third holding experiment was begun 4 May 1973. This population was fed two or three times daily with frozen brine shrimp. Samples were obtained weekly between 4 May and 6 July. We examined sagittae from animals collected 25 May and 8 June 1973.

Wild populations of larval, juvenile, and adult nehu were sampled 13 times in Kaneohe Bay between 19 March 1972 and 13 July 1973 to obtain estimates of growth rates at various seasons. Although a second species of *Stolephorus* (*S. buccaneeri* Strasburg) occurs in Hawaii, larvae of this species have not yet been collected in the southeastern end of Kaneohe Bay (Watson and Leis 1974; W. Watson pers. commun.).

After extraction, the sagittae were cleaned and etched for up to 3 min in a 1% solution of HCl, then washed and mounted whole on glass slides with the mounting medium Euparal[2] and covered with glass cover slips. Short lengths of monofilament line were used to prevent the contact of the specimen by the cover slide. Although the smallest growth increments are microscopically discernible immediately after extraction their detection was enhanced after about 30 days of clearing in the mounting medium. Sagittae used in the first holding experiment and those collected from Kaneohe Bay and Pearl Harbor during spring 1972 were placed in glycerine on slides and covered. Some erosion of the sagittae edges was noted after about 5 mo, and this practice was discontinued after the first experiment. Slides were either labeled with date of collection and length of fish or assigned a five digit random number for identification.

Our initial counts were taken from thin sections of sagittae taken on the frontal plane. After mounting the sagittae in epoxy resin, the initial plane of polishing was made with rough sandpaper. As the surface approached the desired section, fine wet silicon carbide sandpaper (400 grit) was used. Final polishing of the surface was done with suspensions of aluminum oxide particles having diameters of 15, 5, and 0.3 μm. The section was thinned on the opposite side to a practical thickness and etched in a 1% solution of HCl for variable periods up to 3 min. A few attempts to make acetate peels of the small nehu sagittae sections as described by Pannella (1971) and Pannella and MacClintock (1968) were unsuccessful. We eventually abandoned the sectioning of sagittae because of the time required and the difficulty in obtaining a precise section from the nucleus to the posterior edge of the sagitta.

Sagittae were obtained from larvae less than about 20 mm SL by placing the specimen on a slide and gently teasing the otoliths from the head region. The sagittae were then mounted in Euparal and read immediately. These otoliths tended to clear completely within a few hours, and photographs are the only permanent record of these specimens.

The smallest growth increments of the mounted sagittae were counted with a compound microscope at magnifications of 400-800×. The smallest growth increment in all fish otoliths consists of both an organic and an inorganic layer (Degens et al. 1969). These two layers in the nehu otolith together measure about 1-4 μm thick. A zoom feature of the microscope was found to be extremely useful. Counts were maintained on a hand tally.

Enumeration of the smallest growth increment layers in whole sagittae is tedious, and reliable counts can be obtained only after a moderate amount of experience has been acquired. Enumeration is, obviously, much easier in sagittae from smaller fishes (Figure 1). Usually, readings cannot be made in a direct line from the nucleus to the selected point on the edge of the sagitta;

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

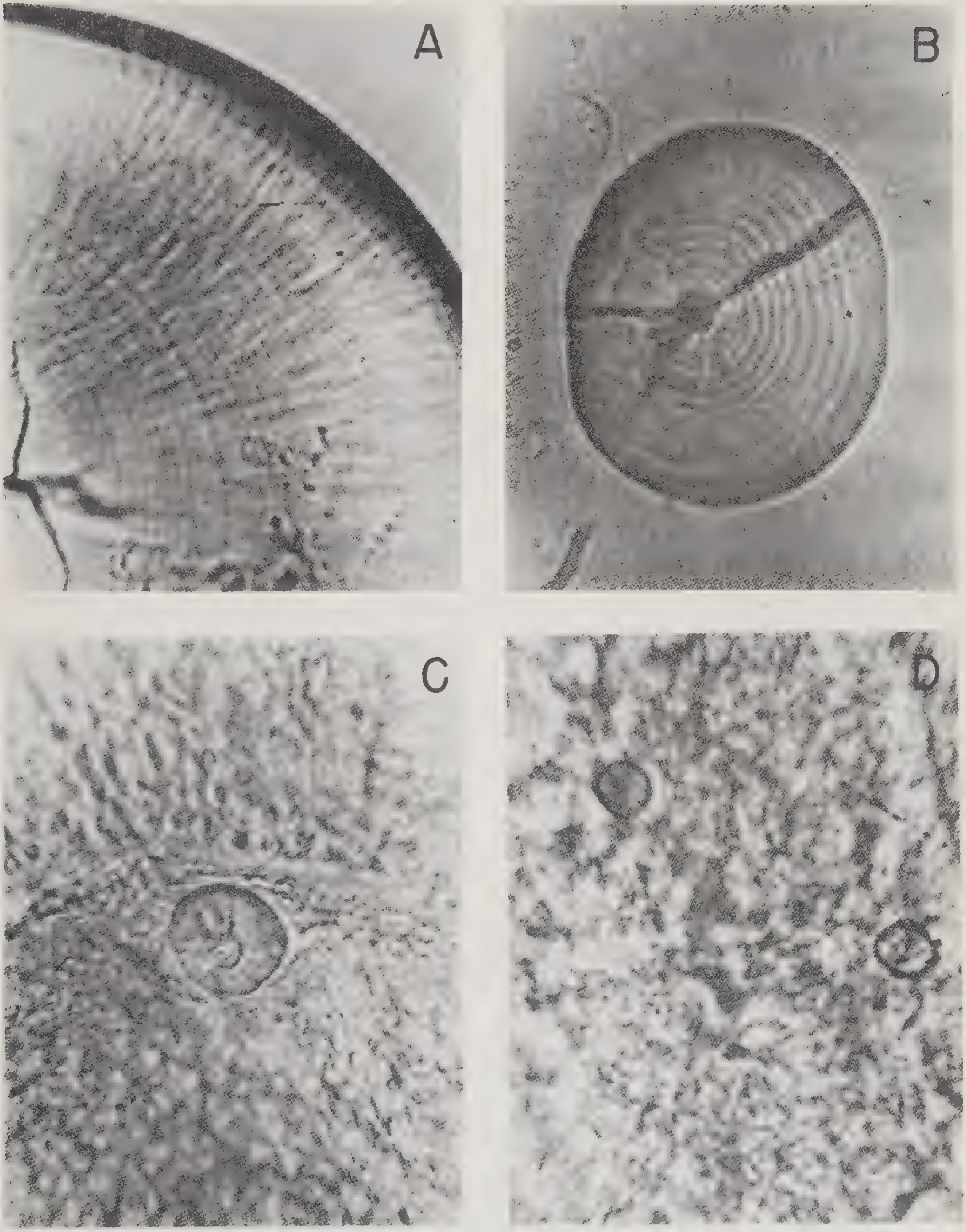

FIGURE 1.—Sagittae of larval *Stolephorus purpureus*. A: Portion of sagitta from a 28.8-mm SL individual with about 65 growth increments. B: 12.6 mm SL, 14 increments. C: 7.3 mm SL, 7 increments. D: 3.9 mm SL, 1 increment.

rather, a somewhat circuitous route must usually be taken from one area of the sagitta to another by following a prominent growth increment.

Each sagitta was counted several times in succession, the number of counts (up to 10) being proportional to the size of the sagitta. Counts were made from the nucleus to the antirostrum, rostrum, and postrostrum (terminology of Messieh 1972). A consistent count for the number of lamellae was then obtained. Verification counts were then made by the same reader at a later time. Verification counts were made by a second reader on 167 otoliths from the second and third holding experiments, as well as randomly selected sagittae representing the wild populations: 26.3% of these counts agreed with the original count; 48.5% differed by less than 1%; 72.5% differed by less than 2%; 86.9% differed by less than 3%; 92.9% differed by less than 4%; and 95.9% differed by less than 5%. Errors of less than 5% were considered acceptable, and the median values of the two readers were then utilized in the analyses. In cases where the results differed by more than 5%, the sagittae were reexamined and either a consensus of opinion reached or the data discarded.

Standard lengths were taken to the nearest 0.01 mm with dial calipers. Sagittae were measured with a micrometer eyepiece.

RESULTS

Holding Experiments

The holding experiments were undertaken as one means to determine if the smallest growth increments observable in the sagittae of nehu represent daily growth increments. We examined sagittae of specimens from samples taken at various time periods after the initial collection to determine if there was an increase in mean number of increments approximating the numbers of days between sampling. (Length data collected from all samples indicate that the length-frequency distributions of most of the captive populations studied were normally distributed.)

The data obtained for each holding experiment were subjected to analysis of covariance and the results are summarized in Table 1 and Figures 2-4. There was homogeneous variance within the samples for each of the three experiments as indicated by Bartlett's test of homogeneity (chi-square values = 0.56, 3.59, and 0.59, respectively).

In the first experiment there were no significant differences between the means of the independent variable (standard length) for each of the three samples at the $P<0.05$ level. There were significant differences between the regression coefficients and the elevation of the regression curves for each sample at the $P<0.01$ level (Table 1, Figure 2).

The significant differences between regression coefficients seems best explained by the effects of captivity. Hypothetically, the regression coefficient of the initial sample of 5 April represents the relationship between number of growth increments and standard length in the wild population. The smaller regression coefficient value of the 21 April sample indicates a slower growth rate of the captive population during the 16-day interval between sampling. This is probably due to less than optimal food supply and/or other effects of captivity. The intermediate regression coefficient value of the 9 May sample indicates that the

TABLE 1.—Summary of analysis of covariance for three holding experiments.

Sampling date	Dependent variable (increments) Unadjusted $\bar{y}$	Adjusted $\bar{y}$	r^2	n	s^2	F ratios Independent variable (standard length)	Regression coefficient	Elevation
5 Apr. 1972	84.9	86.7	0.77	30	38.2			
21 Apr. 1972	101.1	100.6	0.76	24	10.8			
9 May 1972	118.1	116.4	0.74	24	20.6			
First experiment						1.2	5.4^{**}	206^{***}
19 Jan. 1973	114.8	114.0	0.95	25	14.7			
26 Jan. 1973	120.8	121.6	0.85	24	31.1			
Second experiment						0.1	1.3	31^{***}
25 May 1973	124.9	132.1	0.97	23	13.8			
8 June 1973	140.0	133.4	0.95	24	6.1			
Third experiment						34^{***}	1.1	1.1

$^{**}P \leq 0.01$.
$^{***}P \leq 0.001$.

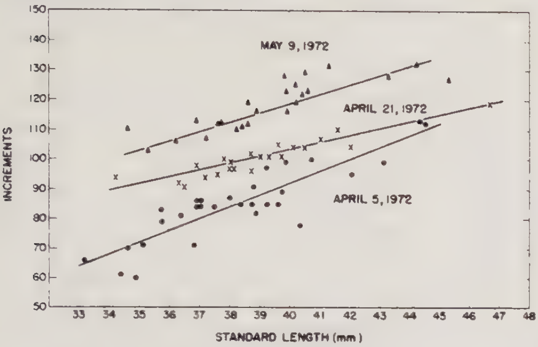

FIGURE 2.—*Stolephorus purpureus*: First holding experiment.

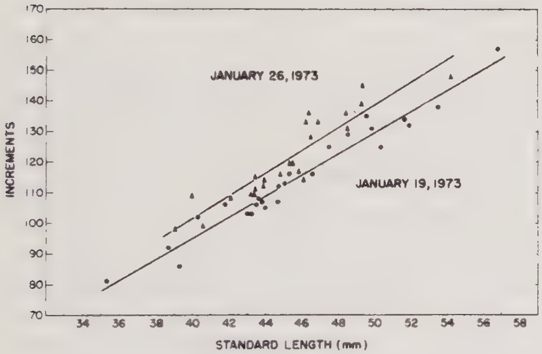

FIGURE 3.—*Stolephorus purpureus*: Second holding experiment.

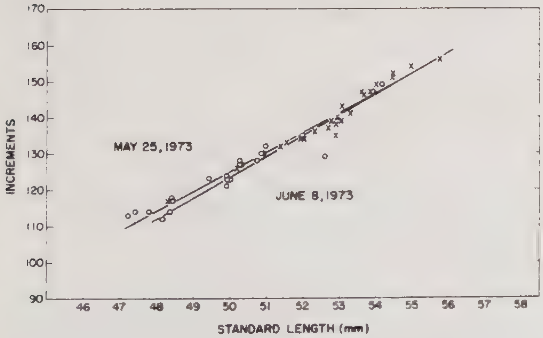

FIGURE 4.—*Stolephorus purpureus*: Third holding experiment.

growth rate has increased in the captive population after 34 days in captivity, but has not reached the value of the wild population from which it was taken.

In the first holding experiment, the second and third samples were collected 16 and 34 days, respectively, after the initial sample. For unadjusted $\bar{y}$ values, these samples differed from the initial sample by 16.2 and 33.2 increments, whereas for the adjusted $\bar{y}$ values, they differed from the initial sample by 13.9 and 29.7 increments (Table 1).

The results of the two samples (collected after more than 30 days in captivity) collected 19 and 26 January 1973, and compared in the second holding experiment, are summarized in Table 1 and Figure 3. There were no significant differences between the means of the independent variables or the regression coefficients at the $P \leq 0.05$ level. The elevations of the two regression curves are significantly different at the $P \leq 0.001$ level. The differences in number of increments between unadjusted $\bar{y}$ values (6.0) and adjusted $\bar{y}$ values (7.6) again closely approximate the expected difference of 7 days between samples.

The results of the samples of 25 May and 8 June 1973 compared from the third holding experiment are given in Table 1 and Figure 4. In this experiment there was a significant difference between the means of the independent variable ($P < 0.001$), but no differences between the regression coefficients and elevations of the two regression curves at the $P \leq 0.05$ level. The significant difference in mean length between the two samples is probably attributable to the increased amount of food provided to the captive population and the resulting high growth rate exhibited throughout the duration of the experiment. Because the treatment significantly affected the independent variable, further examination of the regression statistics is unwarranted. However, if the two samples are subjected to a two-group comparison, there is a significant difference between the mean number of increments for each sample ($P < 0.05$). The difference between the means for each sample (25 May, $\bar{y} = 124.9$; 8 June, $\bar{y} = 140.0$) closely approximates the expected difference of 14 days between samples.

We conclude from the relatively good agreement between the increase in mean number of growth increments and the number of days between collection of samples, that these data from the holding experiments provide direct evidence of the presence of daily growth increments in the sagittae of nehu.

Growth of Sagittae

The total lengths of sagittae from the 5 April and 9 May 1972 nehu samples (the initial sample from the wild population and the 34-day sample) of the first holding experiment were taken in order to examine the effects of captivity on sagittal growth. Four measurements for the 5 April sample were arbitrarily deleted because their values were well below the distribution of the majority of the sample. All 24 measurements from the 9 May sample were utilized. There are significant relationships between sagitta length and fish length for the two samples ($P < 0.001$, r^2 values: 5 April, 0.82; 9 May, 0.70) (Figure 5). The first experiment demonstrated that there was a significant increase in the mean number of increments between the two samples. Analysis of covariance of sagittae lengths indicated that there were no significant differences between the means of the independent variables, regression coefficients, or elevations of the regression curves for the two samples (respective F ratios: 2.5, 1.0, 1.2) presumably because of intrinsic variation, limited precision of measurements, and the relatively short time period between samples. Although there were no statistically significant differences found in the comparison of the two curves, the two regression coefficients exhibit perhaps expectable trends. The lesser regression coefficient and r^2 value for the 9 May sample may be indicative of a decreased growth rate and more variable responses of individuals in the population to the highly variable, and probably less than optimal, conditions of the holding facility. In addition, the differences between the unadjusted and adjusted means of sagittal lengths between the 5 April (1.094 mm; 1.070 mm, respectively) and 9 May (1.176 mm; 1.201 mm, respectively) samples of 0.082 mm and 0.131 mm are to be expected with daily growth increments of about 3-4 μm.

We have noted one apparent example of provisioning rates affecting the growth rates of sagittae of captive nehu. Sagittae from the 19 January sample of the second holding experiment usually exhibited 23-24 distinctive, more widely spaced increments on the edge of the otolith. The numbers of distinctive increments approximately correspond to the number of days during which the daily amount of food provided the sample population was double the initial ration. As might be expected otoliths collected 7 days later in the 26 January sample exhibited 30-31 distinctive increments. Indeed, the wider increments observed after provisioning rates were doubled were much more effective in "labeling" the sagitta than our attempts to accomplish the same objective with Tetracyclene. Possibly, controlled experiments with rapidly growing fish species incorporating this treatment would be a much more expeditious test of the daily growth increment hypothesis.

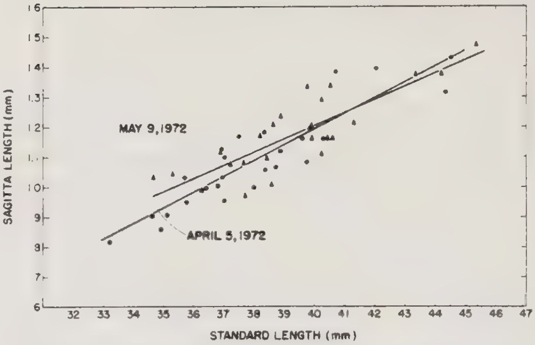

FIGURE 5.—*Stolephorus purpureus*: Growth of sagittae during first holding experiment.

Age and Growth in Wild Populations

We examined larval, juvenile, and adult nehu collected in Kaneohe Bay to obtain an estimate of age and growth of a wild population based on the assumption that the smallest observable growth layers in the sagittae represent daily growth increments. We examined 213 specimens from 13 collections made during most seasons between spring 1972 and summer 1973 (no collections were made in the months November through January). The growth curves obtained from the individual collections are given in Figure 6. Because all individuals in a sample have been exposed to the vagaries of the environment during their observed lifespan, a composite growth curve for all collections is presented in Figure 6F. Although some variation between samples is apparent, the composite scattergram serves as a first estimate of the growth pattern of nehu in Kaneohe Bay.

There are two well-defined segments to the composite growth curve (Figure 6F). Young larvae exhibit exponential growth to a length of about 15-17 mm. At about 20 mm the population enters an almost linear growth phase to about 60 mm. The composite scattergram obscures another, lesser inflection at about 20-30 mm exhibited by the spring 1972 collections (Figure 6A). Yamashita (1951) has demonstrated that nehu have completed larval metamorphosis at about 30 mm. The major inflection at a length of about 17 mm appears to reflect the fact that nehu begin to exhibit exponential growth in body depth at this

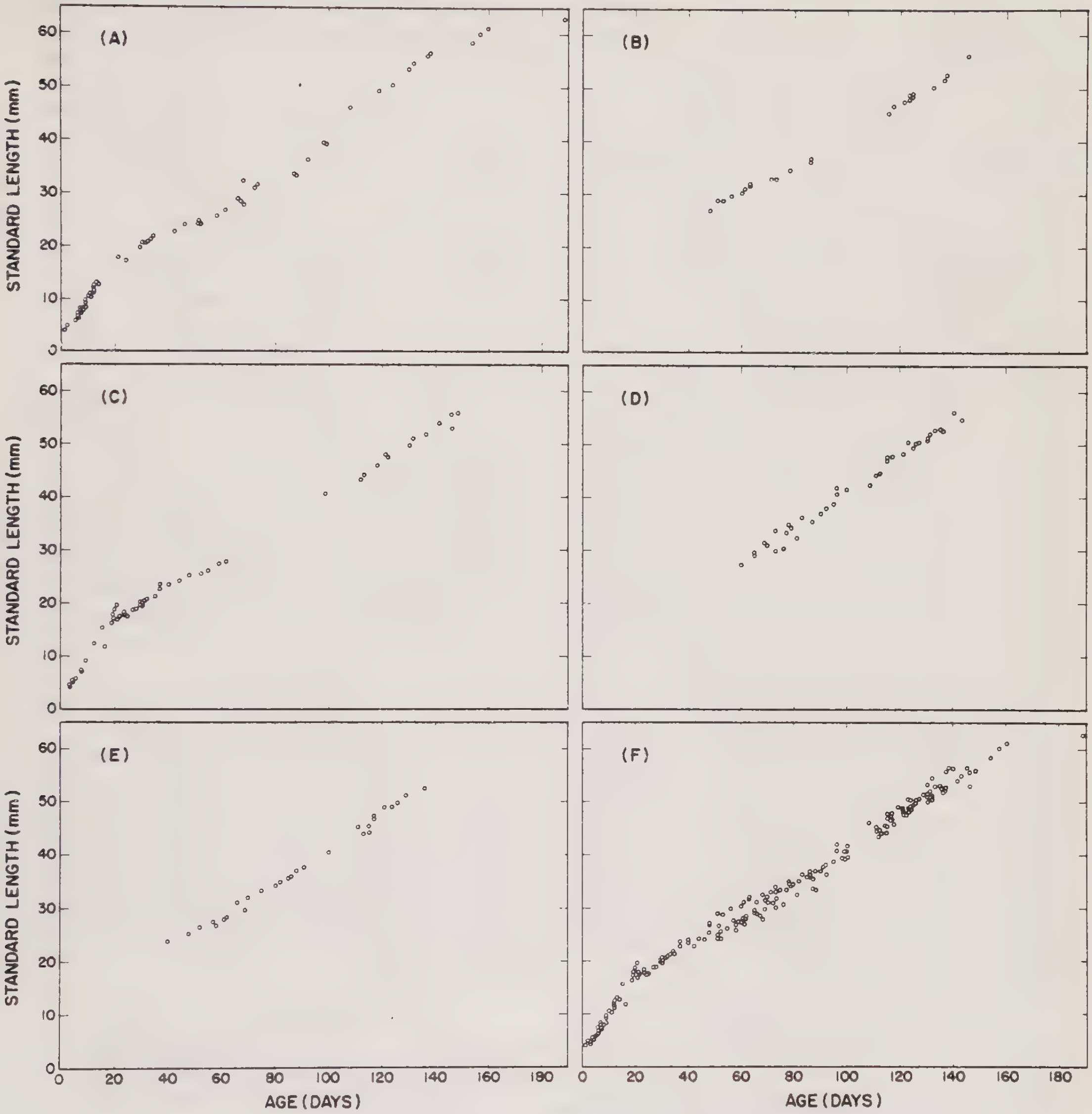

FIGURE 6.—*Stolephorus purpureus:* Age-length relations of 213 individuals from 13 collections in Kaneohe Bay. A: 19 March 1972 (21 individuals, 66-189 days); April 1972 (13, 1-24); 1 May 1972 (11, 6-12); 26 May 1972 (16, 21-68). B: 26 August 1972 (all specimens). C: 7 October 1972 (8, 16-23); 14 October 1972 (23, 19-62); 19 October 1972 (13, 99-148); 25 October 1972 (9,3-9). D: 12 February 1973 (12, 60-87), (11, 115-140); 19 March 1973 (15, 78-125). E: 5 May 1973 (8, 40-69); 13 July 1973 (27, 66-136). F: Composite scattergram of all observations.

size (cf., Nakamura 1970, fig. 4). Thus, much growth of individual nehu is directed to allometric growth of body depth, rather than body length. The growth rate of young nehu (<17 mm) indicated by the composite scattergram is consistent with the estimates of larval growth rates presented by Tester (1951) and Yamashita (1951).

The possibility that the inflection at 15-17 mm is related to a change in diet was examined. Burdick (1969) investigated the feeding habits of larval nehu from hatching to a length of 25 mm in Kaneohe Bay. He found that young nehu less than 5 mm long fed almost exclusively on copepod nauplii. At lengths of 5-7 mm, the diet shifted to a preponderance of small, adult copepods representing two genera. Larvae less than 20 mm fed exclusively during day, at 20 mm they began occasional feeding at night, and when they attained a length of 25 mm they fed regularly at night. None of these changes in feeding habits seem related to the 15-17 mm inflection.

Only one fish, estimated to be 189 days old at a length of about 63 mm, indicated that the Kaneohe Bay population of nehu may enter an asymptotic growth phase at about 60 mm. Obviously, additional collections of older fishes are required to elucidate this portion of the growth curve.

The absence of large adults might be explained by the heavy exploitation of this stock by commercial fishermen. Another possible explanation relates to the observations of Muller[3] on *Stolephorus heterolobus* Rüppell in the Palau Islands of the western Pacific. He found that large spawning adults occur in open lagoon waters 2-4 km offshore over depths of 30-40 m during night. The daytime distribution of these individuals is unknown, but it is thought that they occur near bottom in the open lagoon. In the case of nehu, however, the explanation of an absence of adults in the asymptotic growth phase by invoking an offshore spawning movement is argued against by a recent study demonstrating that this species is capable of spawning at a length of 35-40 mm (Leary et al. in press).

These readings of whole-mounted sagittae from Kaneohe Bay nehu did not reveal any periodic deposition patterns of increments or spawning checks as reported by Pannella (1971).

Geographical Comparison of Growth Rates

One of the more exciting aspects of being able to accurately determine growth rates of young fishes is the tool that it provides to examine the effects of various environmental conditions. As an exercise, we compared the linear segments of the growth curves of two samples (n = 15) of nehu collected during March and April 1972 in Pearl Harbor and Kaneohe Bay (Figure 7). Unfortunately, the differences in size ranges of the two samples and the small sample sizes resulted in significant heterogeneity of variance ($P < 0.05$). The analysis of covariance did indicate, however, that there may be significant differences between the regression coefficients ($P < 0.05$) and elevations ($P < 0.01$) of the two population curves, the Pearl Harbor sample exhibiting a faster growth rate to a length of about 44 mm. Similar, but more intensive, studies should provide a wealth of insight into a variety of aquatic situations.

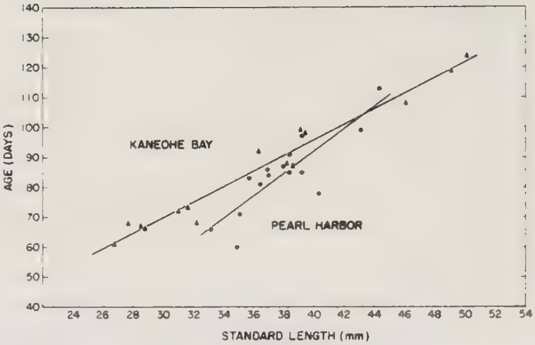

FIGURE 7.—Comparison of *Stolephorus purpureus* growth rates in Pearl Harbor and Kaneohe Bay, spring 1972.

ACKNOWLEDGMENTS

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REEVALUATION OF FISHING EFFORT AND APPARENT ABUNDANCE IN THE HAWAIIAN FISHERY FOR SKIPJACK TUNA, *KATSUWONUS PELAMIS*, 1948-70

Richard N. Uchida[1]

ABSTRACT

Catch per effective trip, used in 1948-64 as an index of apparent abundance of skipjack tuna, *Katsuwonus pelamis*, in Hawaiian waters, is biased because effective trip, defined as one on which fish were caught, underestimates effort. Catch per day fished, calculated from data collected in 1965-70, is a refined index because effort includes days with or without catches. This paper describes the existence of a linear relationship between catch per effective trip and catch per day fished in 1965-70, and a method of estimating the latter from the former in 1948-64 based on this relationship. Fishing intensity, which was measured by standard effective trips in past studies, is calculated in standard days fished. Changes in catch per standard day fished are not associated with changes in relative fishing intensity. Skipjack tuna abundance in Hawaiian waters, therefore, is fishery independent and is probably influenced by availability and strength of year classes.

In the study of the dynamics of any exploited fish population, data on commercial catch and fishing effort can be interpreted in a number of ways, giving various estimates of apparent abundance. The ultimate objective, however, is to obtain the best possible estimate of apparent abundance.

Prior to 1965, studies on catch and effort statistics in the Hawaiian pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis*, defined fishing effort as a "productive" or "effective" trip, that is, one in which skipjack tuna were caught (Yamashita 1958; Shippen 1961; Uchida 1966, 1967). Effective trip underestimated the actual amount of fishing pressure, but it was used because catch report forms used by the fishermen in 1948-65 provided no spaces for recording zero-catch trips.

Zero-catch trips should be considered as effort expended to catch fish because they include time spent searching for schools of fish. But the relative importance of search and fishing time depends on type of gear used. Gulland (1969) used whaling as an example of a fishery where the important measure was time spent searching, the gear being operational only for a few minutes. The other extreme was bottom trawling, where the important measure was time spent catching fish with the gear on the bottom and searching was minimal. Beverton and Parrish (1956) suggested that where searching time is important, the gear may have to be regarded as being engaged in searching for fish but giving no catch until a school is encountered. For pole-and-line fishing, where much time is devoted to searching for schools of fish, Shimada and Schaefer (1956) used the day spent on the grounds as the basic unit of fishing time.

Catch reports of 1965-70 were used to obtain two indices of skipjack tuna apparent abundance: catch per effective trip (*C*/*ET*), calculated from data on trips with catches, and catch per day fished (*C*/*DF*), calculated from total days fished including zero-catch fishing days. The purpose of this study is to determine whether a relationship exists between *C*/*ET* and *C*/*DF*. The importance of the relationship is that it affords a means of converting *C*/*ET* to *C*/*DF* for 1948-64, those years for which no data on *C*/*DF* exist but for which good *C*/*ET* information is available. A corrected measure of apparent abundance, derived from standard days fished instead of standard effective trip, is used to estimate the relative fishing intensity in 1948-70.

COLLECTION OF DATA

Data on skipjack tuna catch and fishing effort were obtained from the Hawaii State Division of Fish and Game, which collects fish catch statistics in the Hawaiian Islands. In addition, catch

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and effort data were also collected routinely at the cannery by personnel of the Honolulu Laboratory, National Marine Fisheries Service. The cannery records, however, were deficient in that they did not provide information on vessels not returning to Kewalo Basin, where the cannery is located, on vessels based on neighboring islands, or on the area of operation.

Catch Reports of 1948-64

The forms for reporting skipjack tuna catch have been revised several times over the years. Essentially, all the different versions used in 1948-64 had spaces for recording the date of landings, the amount of skipjack tuna landed, and the area fished. The date of landing represented an effective trip that may have lasted from one to several days. Because Hawaiian vessels have limited cruising range, a trip usually lasts 1 day. Studies of interview data collected in 1960 showed that of 329 effective trips, 315 or 96% lasted 1 day (Uchida 1967).

Catch Reports of 1965-70

The catch report forms of 1965-70 provided spaces for recording not only the amount of skipjack tuna caught and the area fished, but also the date of each day spent on the fishing ground, a zero catch when no fish was caught, and the number of men aboard per trip. Each entry represented 1 day's fishing. In using data for these years, therefore, days with catches were assumed to be equivalent to effective trips. The sum of days with and without catches was taken as the total number of days fished.

Reporting of Zero-Catch Trips

Review of catch reports and cannery records for 1965-70 showed that some vessels occasionally failed to report zero-catch fishing days. When the number of zero-catch trips recorded in the cannery records exceeded that reported in the catch reports, the difference was assumed to be the number of unreported zero catches. Most vessels reported more zero catches in the catch reports than were recorded in the cannery records; presumably, trips were not recorded at the cannery when a vessel did not return to home port. These catch reports were assumed to be accurate.

Not all unreported zero-catch days were accounted for. In a few cases, vessels failed to indicate a zero catch in the catch report after an unsuccessful day of fishing and also failed to return to Kewalo Basin, site of the cannery and home port of the Honolulu-based fleet. Then, neither the catch report nor the cannery record showed the effort expended.

For Honolulu-based vessels, unreported zero-catch days in 1965-70 varied between 0.5 and 3.8% of the estimated annual number of days fished (Table 1). Differences between reported and estimated number of days fished were not significant ($t = 1.020$; df = 5; $P = 0.36$); therefore the few zero-catch days that went unreported should not seriously affect the data in this study.

TABLE 1.—Total days fished as reported, estimated number and percentage of zero-catch days not reported, and estimated total days fished by Honolulu-based Hawaiian skipjack tuna fishing vessels, 1965-70.

Year	Total days fished as reported (Number)	Estimated zero-catch days not reported		Estimated total days fished (Number)
		Number	Percent	
1965	1,938	10	0.5	1,948
1966	1,773	39	2.2	1,812
1967	1,678	67	3.8	1,745
1968	1,923	42	2.1	1,965
1969	1,469	54	3.5	1,523
1970	1,605	51	3.1	1,656

SOURCES OF VARIABILITY IN FISHING POWER AMONG VESSELS

Fishing power is usually calculated on the basis of a physical feature of the vessel such as gross tonnage or engine horsepower. Differences in fishing power, however, are certainly more complicated than a comparison of these physical attributes. Rothschild (1972) stated that "A considerable portion of the variability in fishing power among fishing units can be attributed to variability in skill of the fishing skipper." Fishing skill cannot be measured easily, but its influence on the fishing power of the vessels should be understood.

Variability in crew size from trip to trip also complicates the comparison of fishing power among the vessels. For example, catch reports showed that crew size in 1970 varied between 5 and 11 men per trip. Frequently, small vessels were fully crewed while large vessels operated shorthanded. The result was that some of the small vessels were outperforming the larger ones in some years.

ANALYTICAL PROCEDURES

In the sections that follow, the procedures used in grouping vessels and fishing areas and in treating the data are discussed.

Classes of Vessels

The difficulties that arise from differences in fishing power among the vessels may be reduced by separating them into relatively homogeneous classes, using physical features such as gross tonnage. It is convenient, therefore, to determine which of the physical features of the vessels is, on the average, proportional to fishing power, and to use it to group the vessels into classes.

In a study covering the period 1952-62, the vessels were grouped into two size classes according to their bait-carrying capacities. Class 1 vessels had capacities up to 3,000 liters per baitwell whereas class 2 vessels had capacities greater than that (Uchida 1967). But the ability of class 2 vessels to catch more fish than class 1 vessels is not necessarily a permanent characteristic. Although baitwell capacity was a good measure of fishing power in the 1952-62 study, it did not reflect fishing power of the vessels satisfactorily after 1962. In 1963-70, some vessels with small bait capacities had catch rates as high as or higher than those with larger capacities. Reevaluation of the data showed that gross tonnage provided a better approximation of vessel performance. *C/ET* and bait capacity were correlated significantly in 8 out of 11 yr in 1952-62, but only in 2 out of 8 yr in 1963-70 (Table 2). Correlation between *C/ET* and gross tonnage, on the other hand, was significant not only in 8 yr in 1952-62, but also in 6 yr in 1963-70. For this study, therefore, vessels of 27 to 44 gross tons were called class 1 and those of 45 to 77 gross tons were called class 2. The selection of the division point between class 1 and class 2 vessels was based on the tendency of *C/ET*, when plotted against gross tonnage, to be closely grouped among class 1 vessels for almost all the years examined. In contrast, *C/ET* of class 2 vessels varied widely in most years.

TABLE 2.—Correlation coefficients of *C/ET* on baitwell capacity and on gross tonnage of Hawaiian skipjack tuna fishing vessels, 1952-70. A single asterisk denotes probabilities between 0.05 and 0.01; two asterisks denote probabilities equal to or less than 0.01.

Year	df	Correlation coefficient of *C/ET* on baitwell capacity	Correlation coefficient of *C/ET* on gross tonnage
1952	23	0.326	0.387
1953	23	0.306	0.275
1954	24	0.602^{**}	0.463^{*}
1955	26	0.498^{**}	0.490^{*}
1956	24	0.390^{*}	0.318
1957	23	0.461^{*}	0.457^{*}
1958	21	0.625^{**}	0.678^{**}
1959	18	0.721^{**}	0.669^{**}
1960	19	0.477^{*}	0.464^{*}
1961	19	0.462^{*}	0.499^{*}
1962	17	0.356	0.528^{*}
1963	18	0.703^{**}	0.757^{**}
1964	18	0.403	0.596^{**}
1965	17	0.368	0.327
1966	15	0.400	0.531^{*}
1967	15	0.593^{*}	0.521^{*}
1968	14	0.434	0.529^{*}
1969	13	0.382	0.516^{*}
1970	13	0.510	0.447

The relationship of fishing power to vessel age and to bait usage cannot be overlooked. Among 8 class 1 vessels fishing in 1963-70, only 1 was built after World War II whereas 9 out of 12 class 2 vessels fishing in 1963-70 were built after the war. The relative comfort and reliability of most class 2 vessels undoubtedly accentuated the relation between fishing power and tonnage by attracting better captains and fishermen. Also, the difference between vessel classes in the amount of bait used was pronounced. Whereas class 1 vessels used an average of 8.3 buckets of bait per day fished, class 2 vessels averaged 12.3 buckets.

Each year in the Hawaiian fishery the same few vessel captains vie for the distinction of being captain of the "top boat." Variability in skill among captains, therefore, complicated the comparison of fishing power among vessels. Furthermore, captains and crew frequently shifted from one vessel to another, taking their fishing skills with them. In 1965-70, for example, a minimum of nine vessels changed captains and the transfer of a highly regarded captain usually involved the transfer of part of his former crew. The shifting of personnel caused some high-producing vessels to become low- or marginal-producers.

Fishing Areas

After the establishment of the vessel classes, the data within each size class were then grouped into inshore and offshore fishing areas. In the Hawaiian fishery, the deployment of fishing effort and the resulting catches are recorded according to a statistical area system that was established for Hawaiian waters by the Hawaii State Division of Fish and Game in 1947 (Uchida 1970). Basically, three general areas are recognized. The first extends from the coastline to just outside the reef, a distance of about 4 km, and the second extends from 4 to 37 km. Combined and called inshore for this study, these two areas are made up of relatively small statistical areas of unequal sizes. It has been estimated that about 80% of the effort and 75% of the skipjack tuna catch are concentrated within these areas (Uchida 1967). Beyond 37 km is the third area, called offshore here; the statistical divisions within it are large and nearly equal in size.

The inshore fishing ground, restricted to waters within 37 km of the coastline, covered roughly 69,000 km². The offshore ground, on the other hand, was restricted only by the range of the vessels, and varied from year to year. In 1948-65, the vessels covered 111,000 km² in their offshore fishing, but many distant offshore areas were visited in only 1 or 2 yr over this period. The offshore areas visited most frequently totaled roughly 69,600 km².

Comparison of Catch Per Effective Trip and Catch Per Day Fished

The monthly catches of skipjack tuna in 1965-70, separated into inshore and offshore areas within each vessel size class, were divided by two different units of effort. One was the number of days with catches, which was assumed to be equivalent to effective trips; and the index derived was *C/ET*. The other was the total number of days fished, which included days of fishing with and without catches; and the index was *C/DF*. The assumption that days with catches was equivalent to effective trips appears justified; Uchida (1967) showed that 96% of the effective trips lasted 1 day.

Figure 1 illustrates the relationship of the monthly *C/DF* (*Y*) against *C/ET* (*X*) calculated for class 1 and class 2 vessels fishing the inshore and offshore areas in 1965. The least squares regression of *Y* on *X* resulted in a close linear fit with the regression line having an angle of 45°.

A good fit between *C/ET* and *C/DF* can be expected because both indexes are small when fishing is poor and large when fishing is good. In Hawaiian waters, periods of high tuna apparent abundance are characterized by the presence of larger schools and more frequent encounters between vessels and fish schools (Uchida and Sumida 1971).

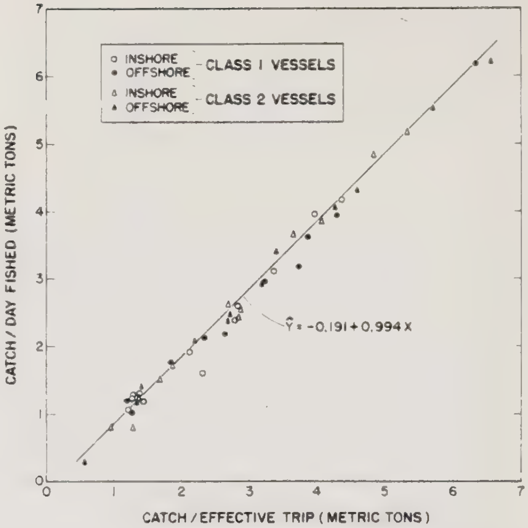

FIGURE 1.—Relationship between catch per effective trip and catch per day fished of Hawaiian skipjack tuna vessels, by areas fished, January-December 1965.

Homogeneity of Data

At the outset of the study, it was decided that one regression equation should be calculated for each area within the size classes. The resulting equations could then be used to estimate *C/DF* from *C/ET* for 1948-64. The decision to calculate one equation for each area by pooling the data for 1965-70 is appropriate, because the data included those years for which skipjack tuna catches from Hawaiian waters were the lowest (1969) and highest (1965) on record. Including data from these 2 yr should provide sufficient low and high values to determine accurately the slope and level of each regression line.

Pooling is appropriate when the samples are homogeneous; therefore, it was necessary to test the hypothesis of homogeneity. Statistical testing of the data, discussed in the following sections, was confined to only one index, *C/ET*, because of the close association between *C/ET* and *C/DF*.

The tests for homogeneity showed that yearly variances of inshore *C/ET* among class 2 vessels differed significantly ($\chi^2 = 11.92$; df = 5; $P<0.05$). A plot of the yearly means and standard deviations, shown in Figure 2A, indicated that they were significantly correlated ($r = 0.883$; df = 22; $P<0.01$). Furthermore, the distribution of *C/ET* was skewed because of many low and few high

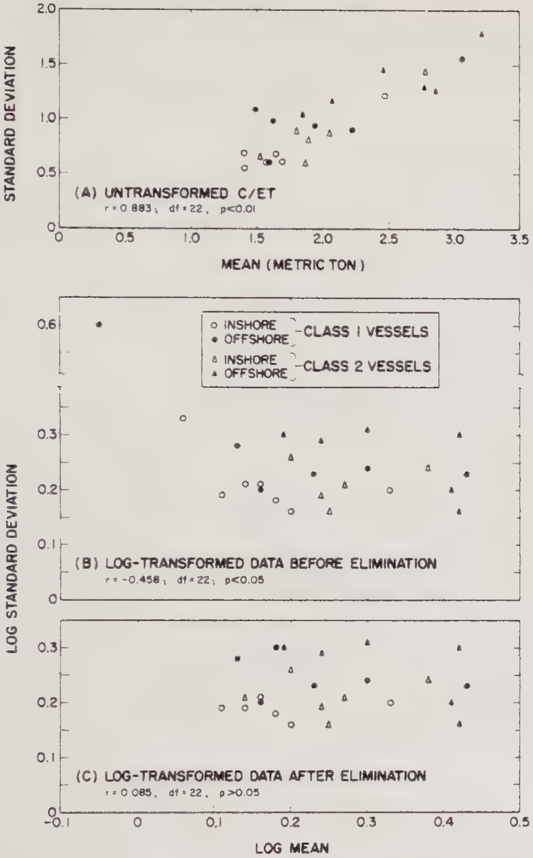

FIGURE 2.—Relationship between mean and standard deviation of catch per effective trip, before and after logarithmic transformation and elimination, by vessel size classes and areas, 1965-70.

values. Because the application of routine statistical procedures requires a normal distribution and independence of the mean and standard deviation, a transformation of the data was required. A logarithmic transformation was selected because the standard deviations tended to be proportional to their means (Figure 2A).

Transformation of the Data

A logarithmic transformation has several theoretical advantages in analyzing catch data (Murphy and Elliott 1954; Gulland 1956). Usually the transformation tends to stabilize the variances and make them independent of the mean. Furthermore, the random components tend to be independently and normally distributed about zero mean and with a common variance.

After the transformation, the means and standard deviations continued to be significantly but negatively correlated ($r = -0.458$; df = 22; $P<0.05$). Examination of the transformed data revealed that there were two points (Figure 2B) that were aberrant and diverged from the cluster of other points. These points represented data for class 1 vessels fishing offshore in 1969 and inshore in 1970. The original monthly catch data showed that the catch rates were affected by very low *C/ET*, all of which were 0.15 MT (metric ton) or less. These catch rates fell close to or beyond $\mu \pm 3\sigma$ and their elimination from subsequent analysis reduced the correlation between the means and standard deviation (Figure 2C) and stabilized the variances ($r = 0.058$; df = 22; $P>0.05$). Tests for homogeneity of variances also indicated that the transformed data for all years could now be grouped by areas within size classes.

Figure 3 shows the frequency distribution and fitted normal curve of the deviations from the mean of log *C/ET* for each area within the size classes. None of the histograms departed significantly from normality when chi-square tests were applied. Therefore, the fit of the normal curve is as good as can be expected (χ^2 ranged from 2.18 to 7.59; $P<0.05$).

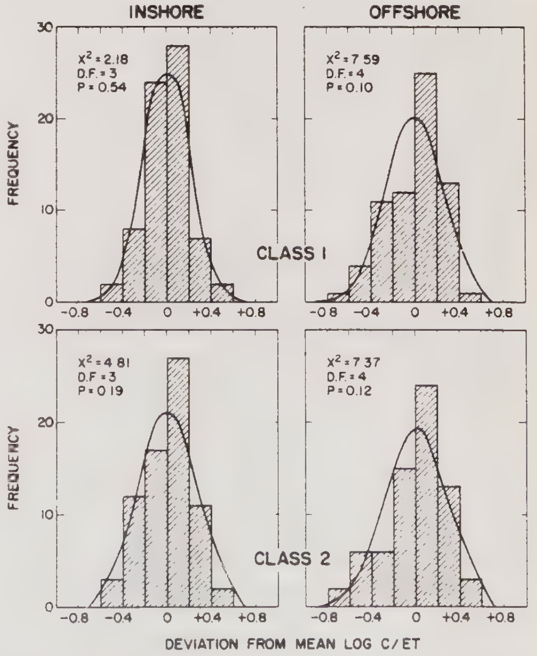

FIGURE 3.—Frequency distribution and fitted normal curve of the deviations from the mean of log C/ET.

Differences in Log Catch Per Effective Trip Between Vessel Classes, Between Areas, and Among Years

A factorial analysis of variance in a randomized complete-block design was used to test whether significant differences occurred in log *C/ET* between vessel classes (blocks), and between areas and among years (main treatment effects). The analysis showed that log *C/ET* with respect to the two vessel classes differed significantly ($F = 12.34$; df = 1 and 265; $P<0.01$). Significant differences in log *C/ET* also occurred with respect to inshore and offshore areas fished ($F = 9.38$; df = 1 and 5; $P<0.05$). Furthermore, the results showed significant differences occurred among years fished ($F = 9.45$; df = 5 and 5; $P<0.05$). A Duncan multiple-range test (Steel and Torrie 1960), with Kramer's (1956) extension of the test, determined that a significant difference in the means occurred primarily between 1965 and 1969, years in which there were considerable differences in fishing conditions.

Relation Between Log Catch Per Day Fished and Log Catch Per Effective Trip

Log *C/DF* increased linearly with log *C/ET* in each of the areas within the size classes. Regression lines, fitted to the data pooled for 1965-70, showed that the scatter about the regression lines was relatively narrow; there were, however, a few observations in each set of data that appeared to have large residuals. To assess the validity or appropriateness of the least-squares fitting of log *C/DF* on log *C/ET*, these residuals were analyzed.

Figure 4 shows the scatter diagrams in which the residuals were plotted against log *C/ET* for the four sets of data. With the exception of a few outliers which can be seen as isolated points with extreme negative ordinates, there were no noticeable peculiarities in the distribution of the residuals. The outliers were rejected at a multiple of the standard deviation using a premium of 2.5% (see Anscombe and Tukey 1963). The overall distribution of the residuals after the rejection procedure appeared in the form of a horizontal band, which indicated that the least-squares analysis of the log transformed data was satisfactory.

After the rejection of large residuals, regression lines were fitted to the data as shown in Figure 5. The dashed lines on either side of the regression lines indicate the 95% confidence limits for the estimates of log *C/DF*. The values of the regression equation and correlation coefficient of log *C/DF* on log *C/ET* are given in Table 3.

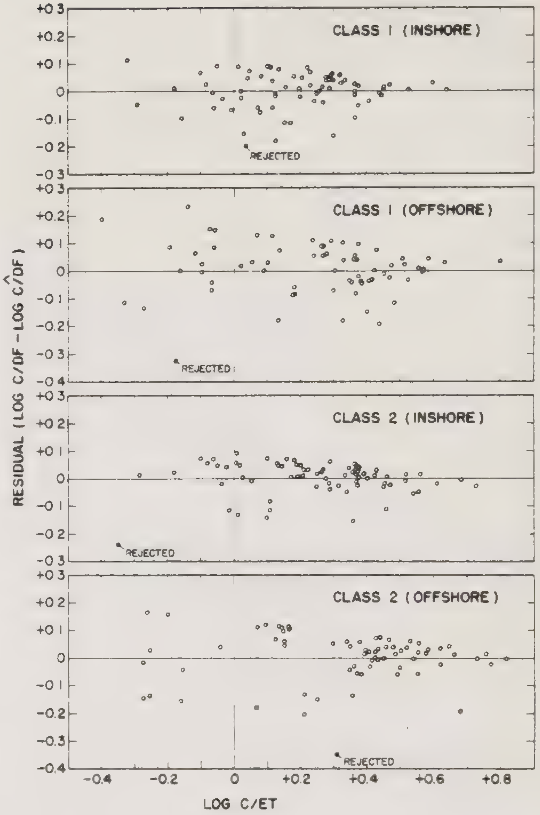

FIGURE 4.—Plots of residuals (log C/DF − log $\widehat{\mathrm{C/DF}}$) against log C/ET for class 1 and class 2 vessels fishing inshore and offshore in 1965-70.

Substitution of values of log a and b into the logarithmic equation $\log_{10}C/DF = \log_{10}a + b\log_{10}C/ET$ and solution of the equation provided estimates of *C/DF* from *C/ET*, by month, for

TABLE 3.—Data on the regression and correlation of $\log_{10}C/DF$ on $\log_{10}C/ET$ in the Hawaiian skipjack tuna fishery, by vessel size classes and areas, 1965-70. Two asterisks denote probabilities equal to or less than 0.01.

Vessel size class	Area	$\log_{10}a$	b	r	df
1	Inshore	−0.11566	1.13915	0.963**	68
	Offshore	−0.12549	1.08370	0.954**	64
2	Inshore	−0.10342	1.13340	0.976**	69
	Offshore	−0.12268	1.13120	0.968**	66

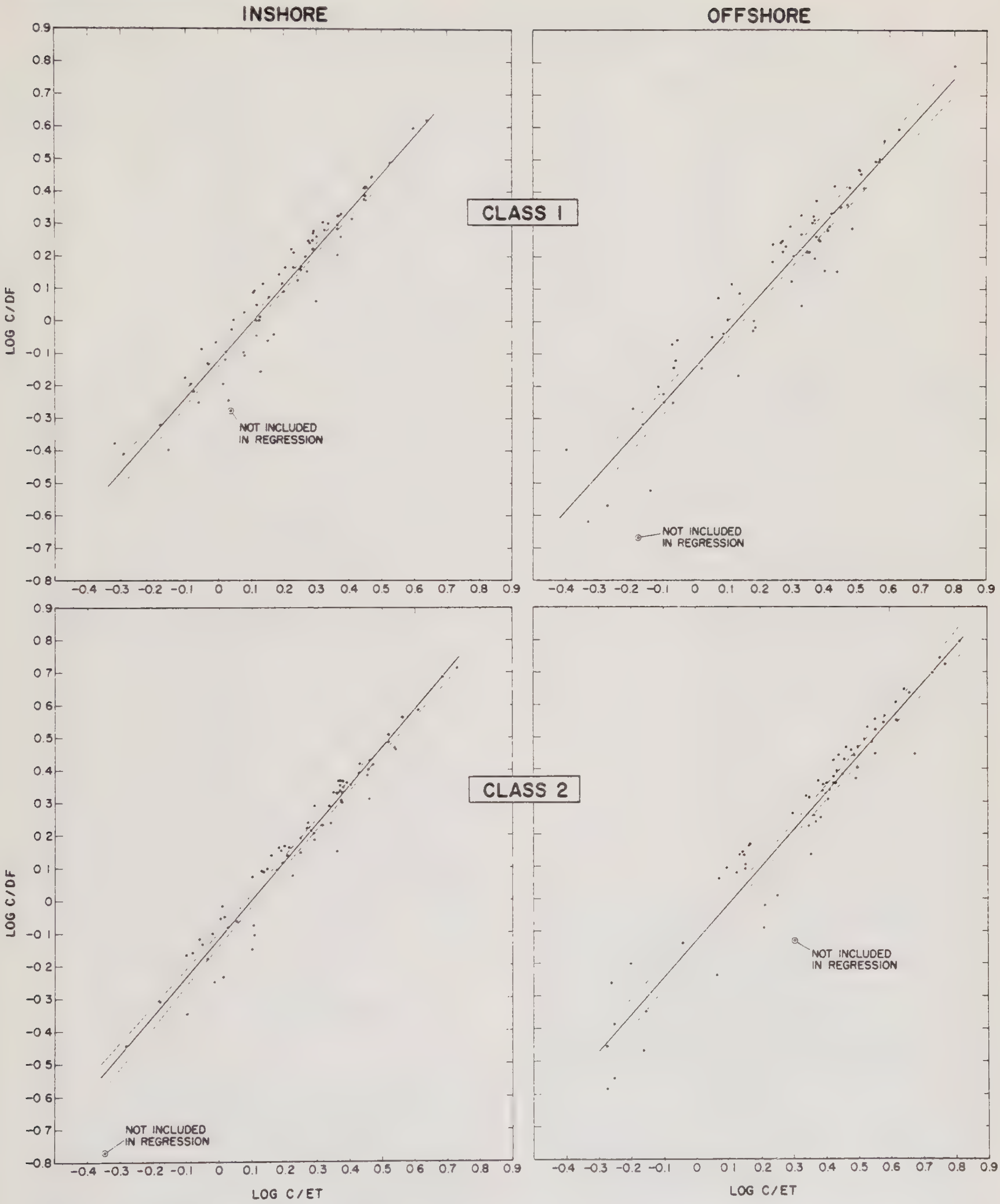

FIGURE 5.—Regression of log C/DF on log C/ET for class 1 and class 2 vessels fishing inshore and offshore in 1965-70.

TABLE 4.—Estimating the number of days fished among class 1 vessels fishing in the inshore area, January-December 1948.

Month	Catch (MT)	Effective trips (No.)	C/ET (MT)	$\text{Log}_{10}C/ET$	$\text{Log}_{10}C/DF$	Calculated C/DF (MT)	Estimated days fished (No.)
January	205.48	77	2.66857	0.42627	0.36993	2.34388	88
February	108.87	73	1.49137	0.17358	0.08207	1.20803	90
March	59.33	72	0.82403	−0.08405	−0.21141	0.61458	96
April	76.91	99	0.77687	−0.10965	−0.24057	0.57468	134
May	133.94	119	1.12555	0.05136	−0.05714	0.87669	153
June	285.80	154	1.85584	0.26854	0.19024	1.54970	184
July	352.30	147	2.39660	0.37959	0.31675	2.07374	170
August	239.72	120	1.99767	0.30052	0.22668	1.68531	142
September	191.07	104	1.83721	0.26415	0.18525	1.53199	125
October	101.31	81	1.25074	0.09716	−0.00497	0.98861	102
November	49.59	44	1.12704	0.05194	−0.05649	0.87802	56
December	19.26	25	0.77040	−0.11328	−0.24470	0.56923	34
Total	1,823.58	1,115					1,374

1948-64. For example, Table 4 shows the data used in the computations and the results obtained among class 1 vessels fishing the inshore area in 1948. C/ET was derived from the equation,

$$C/ET\ (\text{col. }3) = \frac{\text{Monthly catch (col. 1)}}{\text{Number of effective trips (col. 2)}}$$

and converted to logarithms (col. 4). Log C/DF (col. 5) was derived from the equation,

$$\log C/DF = \log a + b \log C/ET$$

and converted to C/DF (col. 6). Days fished were estimated from the equation,

$$\text{Days fished (col. 7)} = \frac{\text{Monthly catch (col. 1)}}{C/DF\ (\text{col. }6)}.$$

Standardization of Catch Per Day Fished

A method of standardizing effort of different size classes of vessel has been discussed by Shimada and Schaefer (1956) for the eastern Pacific yellowfin and skipjack tuna fishery. I used a similar method to estimate relative fishing power of class 1 vessels in the Hawaiian fishery so that their unit of effort was comparable to that of class 2 vessels, which were selected as the standard size class (Uchida 1966, 1967). Briefly, the method involves the use of correction or efficiency factors that are calculated from C/DF of the vessel size classes. Efficiency factors adjust the fishing effort of one size class to that of a standard class. For example, under conditions of equal abundance, the class 1 vessels can be expected to produce a smaller catch than the class 2 vessels. From the catches of the two classes, the fishing power of class 1 vessels can be determined relative to class 2, the standard class, for a given fishing area.

To illustrate the calculation of efficiency factors and the standard unit of effort, the annual C/DF given in Table 5 by vessel size classes and areas were used. In 1948, the efficiency factor for class 1 vessels fishing inshore was $1.33/1.78 = 0.747$ and for offshore was $2.07/3.46 = 0.598$. The efficiency factors for class 2 vessels were fixed at 1.000 for all years. The mean efficiency factor, 0.668, is the geometric mean of the inshore and offshore values. The geometric mean is appropriate for averaging ratios.

Varying from 0.59 to 0.82 (rounded) and averaging 0.71 in 1948-70, the efficiency factors demonstrated not only the greater capability of class 2 vessels, but also the wide variability of the factors from year to year. There was no evidence that the efficiency of class 1 vessels increased or decreased relative to class 2 vessels. Therefore, neither the efficiency of the standard class nor that of class 1 vessels has been altered by the loss of the less efficient or marginal vessels.

MEASURES OF APPARENT ABUNDANCE AND FISHING INTENSITY

Estimate of the apparent abundance of skipjack tuna on the fishing grounds, expressed as catch per standard day fished (C/SDF), can be calculated from efficiency factors and the total number of days fished for each of the two classes of vessels. For example, in 1948 there were an estimated 1,444 fishing days among class 1 vessels and 829 days among class 2 vessels. The standard days fished is the sum of the products of the mean efficiency factor and the total number of fishing days of the size classes. C/SDF is found by,

TABLE 5.—Catch per day fished inshore and offshore among class 1 and class 2 vessels, class 1 efficiency factors, and their geometric mean, 1948-70.

	Inshore			Offshore			
Year	Class 1	Class 2	Efficiency factors	Class 1	Class 2	Efficiency factors	Geometric mean
1948	1.33	1.78	0.747	2.07	3.46	0.598	0.668
1949	1.56	2.24	0.696	2.54	4.12	0.616	0.655
1950	1.34	1.74	0.770	2.10	3.38	0.621	0.692
1951	1.64	2.59	0.633	2.60	3.58	0.726	0.678
1952	1.31	1.66	0.789	1.31	2.19	0.598	0.687
1953	1.53	1.98	0.773	2.37	2.69	0.881	0.825
1954	1.36	2.54	0.535	2.89	3.80	0.760	0.638
1955	1.39	1.99	0.698	2.08	2.32	0.896	0.791
1956	1.90	2.36	0.805	2.30	3.27	0.703	0.752
1957	1.18	1.63	0.724	1.28	1.61	0.795	0.759
1958	1.17	1.87	0.626	1.79	2.36	0.758	0.689
1959	1.97	3.03	0.650	2.37	2.91	0.814	0.728
1960	1.32	2.02	0.653	1.94	2.40	0.803	0.727
1961	1.82	2.37	0.768	2.42	4.05	0.598	0.677
1962	1.49	2.45	0.608	2.22	3.43	0.647	0.627
1963	1.17	1.77	0.661	1.87	3.55	0.527	0.590
1964	1.40	1.69	0.828	2.07	2.90	0.714	0.769
1965	2.39	2.90	0.824	3.32	4.01	0.828	0.826
1966	1.54	1.82	0.846	1.93	2.91	0.663	0.749
1967	1.47	1.84	0.799	1.65	2.31	0.714	0.755
1968	1.57	1.68	0.934	2.04	2.93	0.696	0.807
1969	1.12	1.43	0.783	1.58	2.26	0.699	0.740
1970	1.32	1.74	0.759	1.30	2.36	0.551	0.646

$$C/SDF = \frac{TC_1 + TC_2}{(EF)\,(DF_1) + DF_2}$$

where TC_1 = total catch of class 1 vessels,
TC_2 = total catch of class 2 vessels,
EF = efficiency factor,
DF_1 = days fished among class 1 vessels, and
DF_2 = days fished among class 2 vessels.

In 1948-70, *C/SDF* of skipjack tuna in Hawaiian waters ranged from a low of 1.61 MT in 1957 to a high of 3.29 MT in 1965, but no trend with time was discernible (Table 6; Figure 6).

Relative fishing intensity is estimated from *C/SDF* and the total state catch, which includes catches of part-time as well as full-time vessels:

$$\text{Relative fishing intensity} = \frac{TC_s}{C/SDF}$$

where TC_s = total state catch.

When examined over the 23-yr period, fishing intensity did not decrease appreciably despite a gradual decrease in the number of vessels fishing from a maximum of 28 in 1951 to 15 in 1970. With a reduction in the fleet, which occurred primarily among the older class 1 vessels, fishing intensity would be expected to decline, but it did not. The reason was that the average days fished per vessel per year increased. Class 1 vessels fished an average of 86.1 days per vessel in 1948-58 when their numbers declined from 15 to 10 vessels and 121.2 days in 1959-70 when their numbers further decreased from 8 to 4 vessels (Figure 7). Class 2 vessels have not decreased in number drastically, declining from 14 in 1955 to 11 in 1970. Averaging 86.9 days fished prior to 1964, class 2 vessels subsequently averaged 119.8 days per year.

INTERRELATION OF TOTAL CATCH, FISHING INTENSITY, AND APPARENT ABUNDANCE

The total catch of skipjack tuna, given in Table 6 and shown in Figure 6, fluctuated with *C/SDF* in a similar fashion in 1948-70 (r = 0.902; df = 21; $P<0.01$). For the years studied, then, total catch may be satisfactory as a gross index of changing apparent abundance but may not be suitable in future years because it is obviously sensitive to changes in demand or fishing effort, competition from other fisheries, and economic constraints upon the fishery.

Changes in *C/SDF* are not associated with changes in fishing intensity (r = 0.302; df = 21; $P>0.05$); therefore, the apparent abundance of skipjack tuna in Hawaiian waters is not influenced by changes in the amount of fishing effort expended, but by fishery-independent factors such as variations in availability, which in turn is related to changes in the fishes' habits or

TABLE 6.—Total landings in metric tons (MT) of skipjack tuna in Hawaii, catch per standard day fished, relative fishing intensity, catch per standard effective trip, and relative effective fishing intensity, 1948-70.

Year	Total catch (MT)	Catch per standard day fished (MT)	Relative fishing intensity (Class 2 days)	Catch per standard effective trip (MT)	Relative effective fishing intensity (Class 2 trips)
1948	3,802.96	2.01	1,891	2.30	1,653
1949	4,488.23	2.53	1,773	2.85	1,575
1950	4,314.38	1.99	2,161	2.31	1,868
1951	5,863.37	2.93	2,001	3.28	1,788
1952	3,307.58	1.83	1,806	2.15	1,538
1953	5,470.15	2.14	2,552	2.46	2,224
1954	6,360.13	2.81	2,256	3.16	2,013
1955	4,397.43	1.95	2,248	2.26	1,946
1956	5,049.58	2.59	1,946	2.91	1,735
1957	2,780.66	1.61	1,726	1.90	1,464
1958	3,100.15	1.87	1,652	2.18	1,422
1959	5,630.65	2.93	1,919	3.26	1,727
1960	3,338.46	1.99	1,673	2.30	1,452
1961	4,941.66	2.69	1,835	3.01	1,642
1962	4,270.81	2.56	1,665	2.88	1,483
1963	3,673.86	2.15	1,712	2.48	1,481
1964	4,093.10	1.98	2,065	2.29	1,787
1965	7,328.96	3.29	2,221	3.54	2,070
1966	4,256.82	2.24	1,896	2.52	1,689
1967	3,646.80	1.99	1,832	2.30	1,586
1968	4,227.41	2.04	2,067	2.32	1,822
1969	2,704.94	1.63	1,658	2.02	1,339
1970	3,334.46	1.89	1,760	2.19	1,523

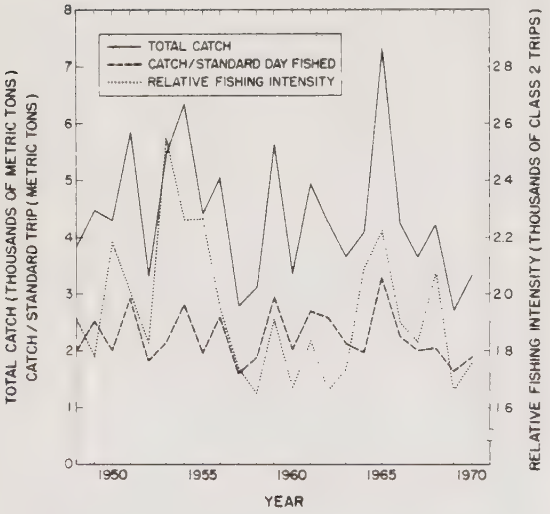

FIGURE 6.—Total catch, catch per standard day fished, and the relative fishing intensity for skipjack tuna in Hawaii, 1948-70.

in the environment, and to the strength of the year classes.

Catch per standard effective trip (*C/SET*) and relative effective fishing intensity, the two indices used in previous studies (Uchida 1966, 1967, 1970), are also given in Table 6. As expected, both *C/SDF* and *C/SET* fluctuated similarly in 1948-70 (r = 0.998; df = 21; $P<0.01$). Likewise the correlation between relative fishing intensity and relative effective fishing intensity was significant, indicating that changes in one paralleled changes in the other (r = 0.982; df = 21; $P<0.01$). It can be concluded that although the use of effective trips in previous studies produced biased results, which deviated from more precise estimates calculated from days fished, its use did

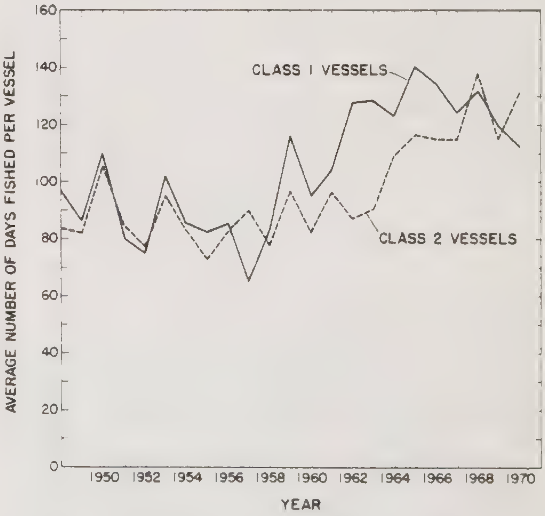

FIGURE 7.—Average number of days fished per vessel per year among class 1 and class 2 Hawaiian skipjack tuna vessels, 1948-70.

not lead to faulty conclusions about the status of the Hawaiian skipjack tuna fishery. The only serious bias appears to be that fluctuations in the *C/SET* were slightly exaggerated and those in effective fishing intensity were dampened.

SUMMARY

The existence of a linear relationship between catch per effective trip and catch per day fished in 1965-70 was described. Based on this relationship, catch per day fished was estimated from catch per effective trip for 1948-64.

Efficiency factors were used to standardize fishing effort of class 1 vessels to that of class 2. The data showed that in 1948-70, efficiency factors for class 1 vessels remained constant relative to class 2 vessels. Fishing intensity, calculated in standard days fished, did not decline over the 23-yr period despite the gradual decrease in the number of vessels fishing. Data from the catch reports showed that in the face of this decline in fleet size, the remaining vessels increased effort by fishing more frequently.

Total catch correlated significantly with *C/SDF*; therefore, it was a good gross indicator of skipjack tuna apparent abundance. Evidence supported the conclusion that in Hawaiian waters, skipjack tuna apparent abundance was not influenced by changes in the amount of fishing effort expended but by fishery-independent factors. And although effective trips as a measure of fishing pressure in previous studies underestimated effort and, therefore, provided a biased estimate of skipjack tuna apparent abundance in the Hawaiian fishery, its use did not lead to faulty conclusions.

ACKNOWLEDGMENTS

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PREHATCH AND POSTHATCH GROWTH OF FISHES— A GENERAL MODEL

JAMES R. ZWEIFEL AND REUBEN LASKER[1]

ABSTRACT

The developmental stages of fish eggs and the growth of larval fishes of several species can be represented by a Gompertz-type curve based on the observation that in widely different living systems, exponential growth tends to undergo exponential decay with time. Further, experimental studies and field observations have shown that the effect of temperature on the growth process follows the same pattern, i.e., the rate of growth declines exponentially with increasing temperature. Evidence suggests that prehatch growth rates determine ideal or optimum trajectories which are maintained after hatch in the middle temperature range but not at either extreme. Also, posthatch growth exhibits a temperature optimum which is not apparent in the incubation period. These studies have also shown that for the same spawn both the prehatch and yolk-sac growth curves reach asymptotic limits independent of temperature. Other biological events (e.g., jaw development) occur at the same size for all temperatures.

The growth of post-yolk-sac larvae follows a curve of the same type and hence the posthatch growth trajectory may be represented by a two-stage curve. For starving larvae, the second stage shows a decline in size but maintains the same form, i.e., the rate of exponential decline decreases exponentially with time.

Recent success in spawning and rearing marine fish larvae at the Southwest Fisheries Center (SWFC) (Lasker et al. 1970; May 1971; Leong 1971) has made possible a much more fundamental examination of the growth process than has heretofore been possible. Controlled laboratory experiments can now be utilized to investigate both the inherent nature of the growth process as well as the effect of some environmental factors.

Considerable care is required, however, in constructing a model[2] which is meaningful both mathematically and biologically. For example, almost all growth models currently in use can be derived as variations of the differential equation:

$$\frac{dW}{dt} = \eta W^{m} - \kappa W^{n} \tag{1}$$

or

$$\frac{dL}{dt} = \eta' L^{m'} - \kappa' L^{n'} \tag{1a}$$

(von Bertalanffy 1938; Beverton and Holt 1957; Richards 1959; Chapman 1961; Taylor 1962) where W is weight, L is length, and η, κ, m, n, m', and n' are arbitrary constants. These are the equations used most often to describe growth as a function of anabolic and catabolic processes of metabolism. The rate of anabolism, η, is considered to be proportional to W^m and the rate of catabolism, κ, proportional to W^n. Equation (1a) requires, in addition, the allometric relationship $W = qL^p$, where again q and p are arbitrary constants. In practice a dilemma arises from the fact that while such models yield a good empirical fit to the data, the estimates of parameters η and κ are often negative, thereby negating the assumptions on which the model is based. For $n = 1$ and $m = 0, 1, 2$, respectively, Equation (1) gives rise to the von Bertalanffy growth in length, Gompertz, and logistic growth functions. Although we have not as yet made any extensive comparisons, the fact that for $m > 1$ and $n = 1$, η and κ must be negative, suggests that in many instances the Gompertz and logistic rather than the von Bertalanffy functions may provide more appropriate models of fish growth. In particular, the simple von Bertalanffy growth model has no inflection point and hence curves such as the generalized von Bertalanffy, Gompertz, or logistic must be used when an inflection in the growth trajectory is evident.

Laird et al. (1965) have presented a Gompertz-type mathematical model of growth based on the

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[2] A model is here conceived to be a mathematical representation of change in length or weight with time under measureable environmental conditions.

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observation that the specific growth rate dW/Wdt of animals and their parts tends to decay exponentially with increasing age. They have shown that this relation offers a practical means of analyzing the growth of parts of embryonic and postnatal animals (Laird 1965a), the growth of tumors (Laird 1964, 1965b), whole embryos of a number of avian and mammalian species (Laird 1966a), and early stages of postnatal growth of a variety of mammalian and avian organisms (Laird 1966b). Further, Laird (1966b, 1967) has shown that postnatal growth of a variety of mammalian and avian organisms can be fitted by compounding this model with a linear growth process beginning at birth and extending on beyond the asymptotic limit of the underlying Gompertz growth process. Overall growth is assumed to be genetically determined by programming only the initial specific growth rate and the rate of exponential decay, these governing growth processes then act on a genetically determined original mass to produce the observed course of growth to a final limiting size characteristic of the species and individual.

Mathematically, these assumptions are described by the two equations:

$$\frac{dW(t)}{dt} = \gamma(t)W(t)$$

and[3]

$$\frac{d\gamma(t)}{dt} = -\alpha\gamma(t)$$

which have the solution

$$W(t) = W_0 e^{\frac{A_0}{\alpha}(1-e^{-\alpha t})}, \qquad (2)$$

where W_0 is weight at $t = 0$, A_0 is the specific growth rate at $t = 0$, α is the rate of exponential decay and the specific growth rate at time t, $A_t = A_0 e^{-\alpha t}$.

Laird et al. (1965) indicated that an additional growth component not included in the Gompertz equation may be due to the accumulation of products that are not self-reproducing or to renewal systems that are not in exact physiological equilibrium and suggested the compound growth curve:

$$W = W_G + \beta \int_0^t \frac{W_G}{M}\, dt \qquad (3)$$

where W_G is the mass due to the Gompertz growth process, β is the rate of linear growth, and M is the asymptotic limit of the growth process. She also suggests that this linear process starts in the early embryonic period, if not at conception. For the age interval covered in this paper, however, the linear growth component ($W - W_G$) was not found to be important.

Several characteristics of the curve are worthy of mention:

1. The asymptotic limit M is $W_0 \operatorname{Exp}(A_0/\alpha)$.
2. The point of inflection $(t_I, W_I) =$ $$\left[\frac{1}{\alpha}\ln(A_0/\alpha),\ W_0 \operatorname{Exp}\left(\frac{A_0}{\alpha} - 1\right)\right].$$
3. The zero point on the time scale may be shifted to any point t_Δ without changing the form of the equation with new parameters $W_\Delta = W(\Delta)$, $A_\Delta = A_0 e^{-\alpha\Delta}$ where α remains unaltered.

The fundamental concept of the Laird-Gompertz model is one of change in weight or mass with time, being due primarily to the self-multiplication of cells and genetically determined limitations on the growth parameters. The use of length as the measured variable is thus a matter of convenience due to the fact that weight measurements are much more time consuming, especially in early larval growth, but also in juvenile and adult fishes. As indicated in Equation (1a), if a true allometric relationship existed, the choice would be unimportant. However, all experimental evidence indicates that both length and weight can be described by a Gompertz-type curve. Hence, it can be shown that 1) the growth rate for both changes continually with time and 2) the form of the length-weight relationship will change continually except for two special instances. Laird et al. (1968) has shown that this occurs only when the rates of exponential decay are the same and either the two measured variables begin growth at different times at the same initial rate or at different rates at the same time. In all other cases the allometric plot will be nonlinear. For

$$L = L_0 e^{K_L(1-e^{-\beta t})}$$

and

$$W = W_0 e^{K_W(1-e^{-\alpha t})}$$

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[3] In the usual Gompertz representation the rate of exponential growth is assumed to decline logarithmically as W approaches the asymptote $M = W_0 e^{\frac{A_0}{\alpha}}$, i.e., $\frac{dW}{dt} = \alpha W \ln(M/W)$.

the length-weight relationship is

$$\ln W = \ln W_0 + K_W\left[1-\left(\frac{K_L-\ln(L/L_0)}{K_L}\right)^{\alpha/\beta}\right]. \quad (4)$$

Only when $\alpha = \beta$ does the relationship reduce to the linear form

$$\ln W = \ln W_0 + \frac{K_W}{K_L}\ln(L/L_0).$$

As shown in Figure 1, departure from linearity will not always be great, but for extrapolation the effect of overestimation at larger sizes may become serious.

Throughout this paper, growth will, by necessity, be measured in terms of length rather than weight even though the model equation is developed from the opposite point of view. It should be remembered, however, that no allometric relationship is assumed, i.e., no relationships among the two sets of parameters are assumed except as they are jointly a function of age.

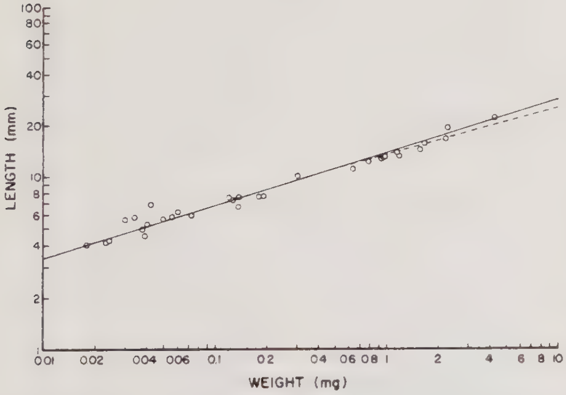

FIGURE 1.–Length-weight relationship in larval anchovies: Solid line fitted from log $W = a + b$ log L; dashed line fitted from Equation (4); estimates are coincident up to 10 mm.

INITIAL ESTIMATES

Equation (2) may be rewritten as follows:

Let $$K = A_0/\alpha$$

and $$M = W_0e^K,$$

then $$W(t) = Me^{-Ke^{-\alpha t}},$$

or $$\ln[-\ln(W(t)/M)] = \ln K\text{-}\alpha t,$$

and hence the logarithm of the logarithm of the ratio of size to the asymptotic limit M with the sign changed will be linearly related to time t with parameters ln K and $-\alpha$. W_0 may be obtained from the relationship $\ln M = \ln W_0 + K$. Note: For decreasing curves, use the reciprocal of the observed values.

VARIABILITY, ESTIMATION, AND TRANSFORMATION BIAS

It is an unfortunate circumstance that the determination of the "best" estimation procedure can rarely be separated from the determination of the "best" mathematical model, i.e., there is no recognized best estimation procedure except in some specialized instances. This is brought about by the fact that almost all parametric estimation procedures assume some information concerning the form and stability of the "error" distribution. This requires, at the very least, the knowledge that the variance is constant and, at the most, the exact form of the error distribution. Since the term "error" in the biological sciences takes a meaning quite different from that in the physical and mathematical sciences in that it represents, in the main, natural variability rather than measurement or experimental error and since natural variability is large (especially so in cold-blooded organisms), few a priori assumptions can be made.

Since most estimation procedures assume a normal distribution of errors at each point along the curve with equal variance (homoscedasticity), the obvious approach, when no more plausible alternative is available, is to fit the situation to this mold.

Some general recommendations are helpful. "Although no clear rule may be safely offered for the taking of logarithms to reduce data to manageable configurations, nevertheless, this transformation (logs) is probably the most common of all. Almost all data that arise from growth phenomenon, where the change in a datum is likely to be proportional to its size and hence errors are similarly afflicted, are improved by transforms to their logarithms" (Acton 1959: 223). Specifically, it can be shown that the logarithmic transformation will induce homoscedasticity in those instances where the standard deviation is proportional to the population mean, i.e., $\sigma = \beta\mu$ or $\log \sigma = \log \beta + \log \mu$. Hence, a plot of $\log \sigma$ on $\log \mu$ will have a slope of unity and the antilog of the intercept will define the proportionality constant. Plots of $\log \sigma$ on $\log \mu$ were made for several experiments where data were available for extended periods of time. None of the regression coefficients was significantly different from unity. These experiments cover a variety of life stages and environmental situations from controlled laboratory experiments on larval anchovies (Lasker et al. 1970) to large tank feeding of anchovies captured from the wild at 75 mm (Paloma, SWFC, unpubl. data) to samples of adult sardines obtained from bait boats (Lasker 1970). Growth for the 75-mm anchovies was slow and much more uniform than for the other experiments as indicated by the mean square errors in Table 1. The analysis of covariance (Table 1) shows no difference in slope for either length or weight from larval, juvenile, and adult fishes. The average slopes are 0.9981 for larvae and adults and 1.1061 for juveniles. With a slope of unity, the proportionality constant can be estimated by Exp ($\overline{\ln\sigma} - \overline{\ln\mu}$). The results from the several experiments are shown below:

	σ/μ	
	Length	*Weight*
Lasker et al. (1970):		
Experiment 1	0.12	0.39
Experiment 2	0.12	0.33
Paloma[4]	0.06	0.20
Lasker (1970)	0.04	0.13

Not unexpectedly, variation in weight exceeds that of length and both decrease with increasing age.

The question of normality and its relationship to homoscedasticity is more tenuous, but again some help is available. In practical work, it is generally assumed that both x and $\log x$ can be regarded as normally distributed as long as the coefficient of variation $C = \sigma/\mu < \frac{1}{3}$ or $\sigma_{\log x} < 0.14$ (Hald 1952: 164). This allows transformation for one desideratum without noticeably affecting another.

TABLE 1.—The relationship of mean and standard deviation for both length and weight measurements in fishes.

	$\log \sigma = \alpha + \beta \log \mu$		Analysis of covariance deviations from regression		
	α	β	df	s.s.	m.s.
Larvae and adults:					
Length[1] exp. 1	−1.5568	1.6979	6	0.3308	0.0551
exp. 2	−0.8003	0.8281	8	0.7167	0.0896
Weight[1] exp. 1	−0.4192	1.0373	6	0.1572	0.0262
exp. 2	−0.4852	1.0077	8	0.4241	0.0530
Length[2]	−1.6093	1.0848	60	2.2933	0.0382
Weight[2]	−0.4748	0.7906	60	2.5913	0.0432
		Within	148	6.5134	0.0440
		Between	5	0.1425	0.0285
		Common	153	6.6559	
$F = 0.0285/0.0440 = 0.65$					
Juveniles:					
Length[3]	−1.3975	1.1644	31	0.3658	0.0118
Weight[3]	−0.8000	1.1029	31	0.1511	0.0048
		Within	62	0.5169	0.0083
		Between	1	0.0002	0.0002
		Common	63	0.5171	
$F = 0.0002/0.0083 = 0.02$					

[1] Lasker et al. (1970), larval anchovies.
[2] Lasker (1970), adult sardines.
[3] Paloma: unpublished data available at SWFC, juvenile anchovies.

Paloma (see footnote 4) collected one or two samples per month of laboratory-reared anchovies for a period of nearly 2 yr. Approximately 25 fish were taken for each sample. We examined normality in terms of skewness (G_1) and kurtosis (mean absolute deviation A). Although sample sizes are small, in terms of positive (>mean) and negative (< mean) coefficients, the transformation was effective in normalizing both fish weight and length as shown below:

		L	*log* L	W	*log* W
$G_1(\mu_{G_1} = 0)$	>	19	17	24	16
	≤	14	16	19	17
$A(\mu_A = 0.7979)$	>	18	17	17	17
	≤	15	16	16	16

For these same samples, length and weight were assumed bivariate—log normal and confidence regions were calculated for each sample. On the average, 96% of the observations fell within the 95% confidence ellipse.

In summary, there is strong evidence that the logarithmic transformation will be required to stabilize the variability in all phases of fish growth and that such a transformation will support the assumption of a normal distribution at least in the intermediate size range (75-100 mm) and most likely at other sizes as well.

Seemingly then, the conditions have been met for implementation of either the maximum likelihood or least squares estimation process. However, two problems remain, neither of which has an entirely satisfactory solution. The first, the absence of an explicit solution of the normal equations, arises because the parameters enter the model in a nonlinear manner and, as is usual in situations of this kind, an iterative procedure is required. The one employed for this paper is Marquardt's algorithm (Conway et al. 1970). Procedures such as this are usually justified on the basis that for large samples and independent observations the estimates obtained are "very close" to those which would be obtained by plotting the likelihood function itself (Box and Jenkins 1970: 213). In truth, the small sample bias and variability of such estimates remains unknown. In growth data the second problem is that sequential observations are not likely to arise from entirely independent processes. This fact is usually manifested as a series of runs above and below a fitted curve rather than random variation. One simple explanation is that growth is in reality a series of asymptotic curves and that oscillations around a fitted curve indicate more than one growth cycle. In this case, the basic assumption of the estimation procedure and the likelihood function itself will not be met. No satisfactory solution to this problem has been proposed and none is proffered here. However, since the same larvae were not measured at different ages and since correlated observations usually have little effect on the estimates of mean values, such estimates will likely not be seriously biased. Using these estimates, "goodness of fit" is examined through the magnitude of the residual mean square and the pattern of residuals along the growth curve, rather than using significance tests or confidence intervals.

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[4] Paloma, P. Unpublished data available at SWFC.

One further point often considered but left unsaid is the effect of transformations on the estimated means. Such changes of scale can lead to serious biases and errors in interpretation, especially when the coefficient of variation is large. When the exact form of the error distribution is known the bias can usually be determined mathematically. For the log normal, for example, it is necessary to add one-half of the error mean square before calculating the antilog mean. Unfortunately, in practical work, it is generally impossible without very large samples, to determine the distributional form. As stated above, for many situations, x and $\log x$ can both be considered to be normally distributed. In these intermediate cases, however, the bias correction for $\log x$ will be small so, that as a general rule, one can state that whenever a transformation is made, the correction for transformation bias should be used.

RESULTS

Growth Cycles

Previous work on the growth of larval anchovies (Kramer and Zweifel 1970) suggested that the Laird form of the Gompertz equation might provide a useful model of larval growth. Figure 2 reveals several phenomena found to be almost universal in larval growth: 1) there is a moderate increase in length during the interval following hatch that is followed by 2) a period of minimal growth accompanied by nearly uniform variability, and 3) at the onset of feeding, the mean size increases rapidly with variability proportional to the square of the mean size.

Farris (1959) noted the rapid leveling off in growth following hatch for the Pacific sardine and three other species and approximated the growth rate by two discontinuous curves and indicated that "a more detailed study would probably reveal a nonlogarithmic continuous growth function."

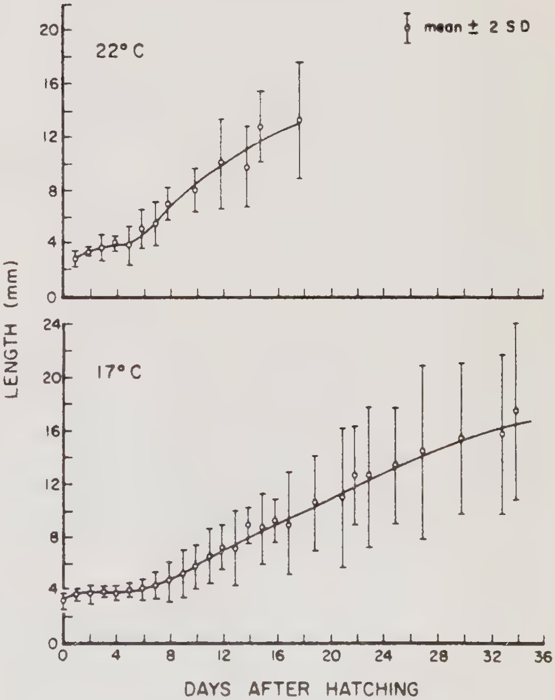

FIGURE 2.–Change in length of yolk-sac and feeding larval anchovies at two temperatures, 17° and 22°C from Kramer and Zweifel (1970); curves are two-cycle Laird-Gompertz.

Although the single stage model used by Kramer and Zweifel (1970) provides an adequate growth curve, two growth cycles are evident: one extending from hatching to the depletion of the yolk sac and the other a more rapid growth at the onset of feeding. Thus, a two-stage model was used to obtain the curves in Figure 2. The fitting procedure is outlined in the Appendix.

It is evident that early larval growth of this species can be represented by a two-stage Laird growth curve. The charcteristics of the growth curves of feeding larvae, i.e., the second cycle, may be related to several environmental factors of which the two most important are probably food ration and temperature. However, an examination of data available on nonfeeding larvae (Figure 3) indicated that even in food-limited situations, change in size may be represented by the two-stage Laird curve.

Growth From Hatch to Depletion of Yolk Sac

The characteristics of the early posthatch growth of larval fishes is more completely described by Lasker (1964). In this series of experiments, growth in length of the Pacific sardine, *Sardinops sagax*, was measured for up to 10 days following hatching at 12 temperatures in the range 11°-21.3°C. The parameters of a single stage Laird curve (Equation 2) were estimated for each of these experiments. Data only up to the day preceding the first decrease in size were used in the calculations.

Even though for such short time series, the parameters are highly correlated due to near-redundancy of one of the parameters, two observations were striking; there was a nearly constant estimated hatching length of about 3.75 mm and a nearly constant estimated maximum length of about 6.1 mm. Accordingly, those experiments with hatching lengths near 3.75 mm and a measured increase in size of at least 3 days were fitted to the reparameterized model:

$$L(t)_T = L_0 e^{K(1-e^{-\alpha_T t})}$$

where $K = A_{0_T} / \alpha_T$

and the T subscript indicates temperature in °C. A plot of α_T on temperature revealed another Laird-Gompertz curve approaching an asymptote at higher temperatures.

A five parameter model:

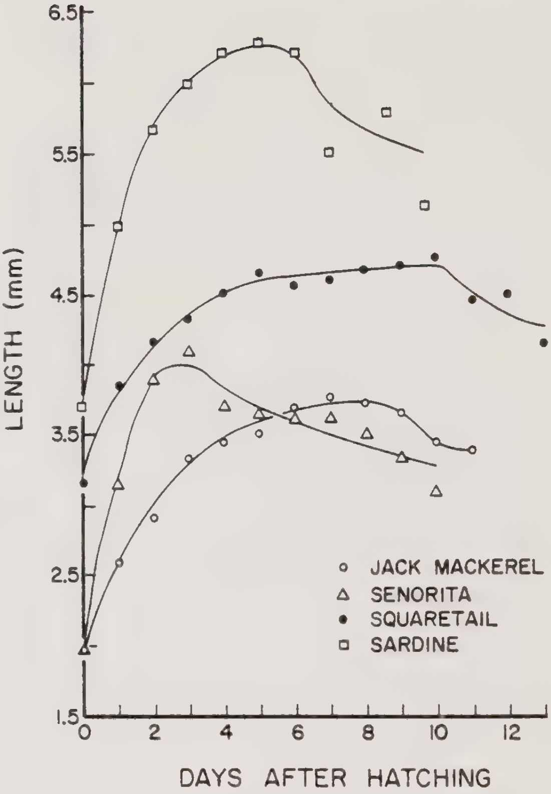

FIGURE 3.–Change in length of yolk-sac and starving larvae; curves are two-cycle Laird-Gompertz.

$$L(t)_T = L_0 e^{K(1-e^{-\alpha_T t})} \tag{5}$$

where $$\alpha_T = \alpha_0 e^{m(1-e^{-\beta T})} \tag{5a}$$

was used to fit the growth data from all experiments and provided an excellent fit except at the highest temperature where growth was always overestimated. This suggested a temperature optimum with growth rates decreasing as the absolute difference $|T - T_{\text{opt}}|$ increases. Following Stinner et al. (1974), who used a different temperature function, we assumed symmetry around the optimum.

Using Equation (5a), the origin of the temperature scale may easily be shifted to the optimum T_{opt} by the relationships:

$$\alpha_{\text{opt}} = \alpha_0 e^{m(1-e^{-\beta T_{\text{opt}}})}$$

and $$m_{\text{opt}} = m e^{-\beta T_{\text{opt}}}$$

and letting $\Delta = |T - T_{opt}|$

we have the symmetric relationship

$$\alpha_T = \alpha_{opt} e^{m_{opt}(1-e^{-\beta\Delta})}. \tag{5b}$$

Substituting Equation (5b) for Equation (5a) and treating T_{opt} as an unknown parameter, a six parameter model was fitted to the growth data with the results shown in Table 2.

TABLE 2.–Growth in length of yolk-sac larvae of the Pacific sardine at several temperatures.

Length					
Observed[1]	Estimated[2]	SE	Age (days)	Temperature (°C)	*N*
3.76	3.72	0.15	0.00	11.00	7
4.30	4.27	0.27	1.00		4
4.78	4.71	0.50	2.00		4
4.97	5.06	0.25	3.00		2
3.77	3.72	0.20	0.00	12.00	9
4.50	4.40	0.24	1.00		11
4.71	4.91	0.29	2.00		8
5.04	5.28	0.44	3.00		6
5.50	5.54	0.36	4.00		3
3.73	3.72	0.16	0.00	13.00	8
4.50	4.55	0.23	1.00		17
4.97	5.12	0.41	2.00		11
5.46	5.49	0.45	3.00		9
4.80	4.72	0.20	1.00	14.00	22
5.39	5.33	0.27	2.00		19
5.65	5.67	0.36	3.00		9
3.93	4.08	0.13	0.30	14.20	11
4.08	4.09	0.13	0.30	14.30	5
5.14	4.89	0.44	1.00	15.00	17
5.59	5.51	0.35	2.00		20
5.96	5.81	0.32	3.00		10
3.71	3.72	0.25	0.00	16.00	21
5.01	5.07	0.25	1.00		19
5.68	5.67	0.26	2.00		23
5.99	5.91	0.15	3.00		11
6.23	6.00	0.11	4.00		9
3.74	3.72	0.22	0.00	16.80	14
5.20	5.21	0.16	1.00		16
5.77	5.78	0.20	2.00		22
6.14	5.97	0.20	3.00		13
3.69	3.97	0.10	0.10	17.80	5
5.27	5.38	0.19	1.00		16
5.86	5.88	0.23	2.00		22
6.06	6.01	0.22	3.00		19
3.71	3.72	0.21	0.00	18.80	4
5.46	5.53	0.18	1.00		18
5.98	5.95	0.21	2.00		25
6.09	6.04	0.15	3.00		18
3.73	3.72	0.10	0.00	19.60	4
5.36	5.58	0.19	1.00		18
5.73	5.97	0.17	2.00		15
5.93	6.04	0.25	3.00		16
5.10	4.83	0.12	0.50	20.50	12
5.46	5.45	0.16	1.00		12
5.43	5.32	0.03	1.00	21.30	3
5.90	6.00	0.13	3.00		5

[1] From Lasker (1964).

[2] Calculated from Equations (5) and (5b) with parameters L_o = 3.716, K = 0.4872, α_{opt} = 1.8523, m = 3.3878, β = 0.0490, and T_{opt} = 19.38.

Growth From Fertilization to Hatch

Coincident to the investigation of early larval growth, a study of the incubation times for the sardine showed that they also could be characterized by a Laird-Gompertz curve. The fitting of Equation (5a) with α_T being incubation time showed no bias at any point along the curve (Figure 4). Unlike the posthatch growth curves, however, no evidence of a temperature optimum was found, i.e., incubation time did not increase at high temperatures. One possible explanation is that larvae which expire cannot be included and hence mortality introduces a negative bias in the estimate of average or median incubation time.

The question arises whether changes in growth rates occur at hatching, i.e., is there a single curve from fertilization to onset of feeding? It can be shown that under the Laird-Gompertz model where growth is approaching a common asymptote from a common origin, i.e. fertilization, the incubation time I_T is simple multiple of the decay rate α_T. From Equation (5) we may solve for the time to hatch I_T at size L_h to obtain:

$$I_T = \ln\left(\frac{K}{K-\ln(L_h/L_0)}\right)/\alpha_T\,.$$

Since incubation times were not available for all temperatures used in the growth experiment, the sardine curve from Figure 4 was used to convert all data taken at temperatures less than optimum to time from fertilization and fitted to Equation (5).

The results for sardines indicated an increasing size at hatch with increasing temperature which was not evidenced by the observed data and an overestimate of size at temperatures less than 14°C. It was thus concluded that a change in growth rate occurs at hatch, the more noticeably at extreme temperatures and that the prehatch curve must be estimated separately.

The parameters of the prehatch growth curves were obtained by fitting the equation

$$L_h = L_0 e^{K(1-e^{-\alpha_T I_T})} \tag{6}$$

to only data obtained less than 12 h following hatch. The average estimated hatching size was 3.73 mm and the asymptotic limit was 6.13 mm. The plot for several selected temperatures is shown in Figure 5. Laird (1965a) has shown that the length scale may be standardized and logically simplified by expressing size relative to the asymptotic limit. Biological events such as

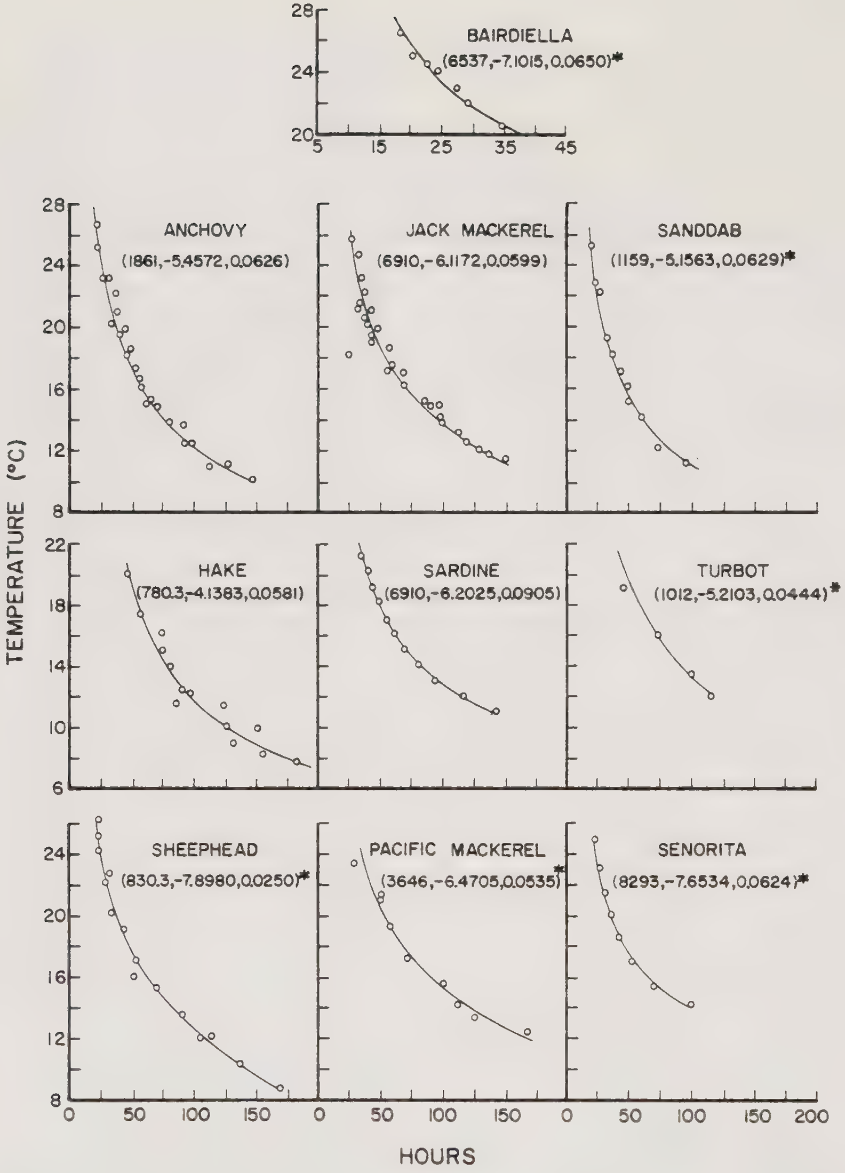

FIGURE 4.—Observed (0) and estimated (curve) (parameters in parentheses are I_0, m, and β for the equation $I_T = I_0 e^{-m(1 - e^{-\beta T})}$ and * indicates time from stage III eggs) incubation times for anchovy, *Engraulis mordax* [combined data from Lasker (1964) and Kramer (unpubl. data) available at SWFC]; hake, *Merluccius productus*; sheephead, *Pimelometopon pulchrum*; bairdiella, *Bairdiella icistia*; jack mackerel, *Trachurus symmetricus*; sardine, *Sardinops sagax*; Pacific mackerel, *Scomber japonicus* (Watanabe 1970); sanddab, *Citharichthys stigmaeus*; turbot, *Pleuronichthys decurrens*; señorita, *Oxyjulis californica*.

developmental egg stages, hatching, and development of the functional jaw occur at fixed points along the curves. Ahlstrom (1943) reported time to several developmental egg stages at different temperatures from field observations. In addition, Lasker (1964) showed incubation times and time to the development of the functional jaw for a wider range of temperatures. Each of these events can be identified as a fixed percentage point in Figure 5 or the estimated value

$$t_{L_T} = \ln \left(\frac{K}{K - \ln (L_T/L_0)} \right) / \alpha_T \qquad (7)$$

as shown in Table 3.

Lasker (1964) found that the functional jaw did not develop at the lowest two temperatures in agreement with the result that the critical size would not be reached until well after yolk absorption.

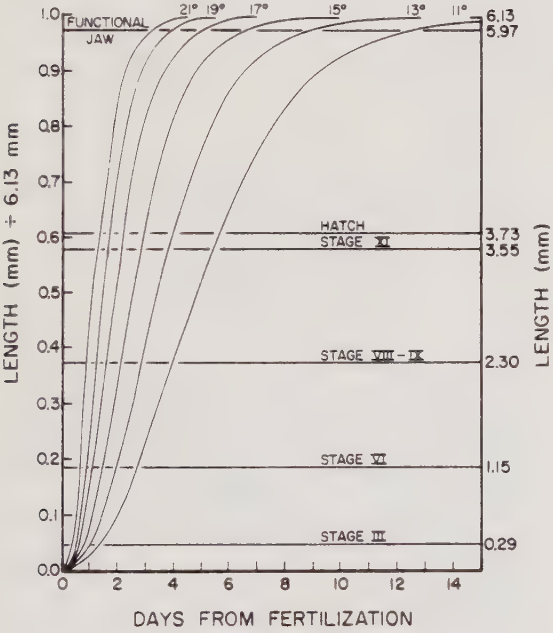

FIGURE 5.–Prehatch growth curves estimated from Equations (5) and (5a) for the Pacific sardine.

Incubation Times

Incubation times were available for several other species. The fitting of Equation (5a) for each species showed no clear bias at any point along the curve (Figure 4). As for the sardine, no evidence of a temperature optimum appeared for any of the species in the temperature ranges used in the experiments. However, it was observed that the decay parameter was relatively constant varying from 0.03 to 0.09 with a mean value of 0.05. When Equation (5a) was fitted with the temperature decay parameter, β, the same for all species, incubation times were closely approximated by Equation (5a) with parameters as shown in Table 4.

The incubation curves used here differ significantly from those calculated from the classical Arrhenius equation: log (incubation time) = $a + b/$absolute temperature. Using this method, nearly all species showed a characteristic underestimate at the temperature extremes and overestimates in the middle range as shown for the northern anchovy, *Engraulis mordax* (Figure 6).

Prehatch Growth Curves for Other Species

In addition to incubation times for the northern anchovy, Kramer[5] recorded time to several developmental egg stages. Also, Lasker (1964) provided time to hatch from stage IV[6] (Table 5). Further, Hunter (pers. commun.) indicates that

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[5] Unpublished data available at SWFC.

[6] Stages of embryological development are those described by Ahlstrom (1943).

TABLE 3.–Observed (Obs.) and estimated (Est.)[1] time in hours to developmental egg stages[2], hatch, and appearance of the functional jaw of the Pacific sardine.

	Ahlstrom (1943)								Lasker (1964)				
Temp. (°C)	Stage III		Stage VI		Stages VIII-IX		Stage XI		Temp. (°C)	Incubation time		Functional Jaw	
	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.	Obs.	Est.
13.5	20.4	20.1	41.8	42.9	62.5	63.2	82.6	85.4	11	140	135	—	—
14.0	18.9	18.6	39.1	39.7	58.3	58.5	77.2	79.0	12	115	114	—	—
14.5	17.4	17.3	36.6	36.8	59.4	54.3	72.2	73.3	13	93	96	213	216
15.0	16.2	16.1	34.3	34.2	50.7	50.4	67.5	68.1	14	78.5	82.4	179	185
15.5	14.9	15.0	32.1	31.9	47.2	46.9	63.1	63.4	15	68.1	71.0	156	160
16.0	13.8	14.0	30.0	29.7	44.0	43.7	59.0	59.1	16	60.2	61.6	136	138
16.5	—	—	28.1	27.7	41.1	40.8	55.1	55.2	17	53.7	53.8	119	121
17.0	—	—	26.3	26.0	—	—	51.5	51.6	18	48.4	47.3	105	106
									19	43.2	41.8	94	94
									20	39.3	39.2	85	84
									21	34.0	33.2	77	75

[1] $L_o = 0.0341$, $K = 5.20$, $\alpha_o = 0.0317$, $m = 6.19$, and $\beta = 0.0489$.

[2] Egg stages are defined in Ahlstrom (1943).

TABLE 4.—Parameters for estimating incubation time I at centigrade temperature T from the relationship $I_T = I_0 e^{m(1 - e^{\beta T})}$ for several fishes where β is the same for all species.

Species	I_0	m	β
Señorita			
Oxyjulis californicus	[1]6,103	−7.9531	0.0527
Bairdiella			
Bairdiella icistia	[1]3,170	−6.8216	0.0527
Pacific mackerel			
Scomber japonicus	3,580	−6.4896	0.0527
Jack mackerel			
Trachurus symmetricus	1,854	−6.2486	0.0527
Pacific sardine			
Sardinops sagax	2,121	−6.2322	0.0527
Northern anchovy			
Engraulis mordax	1,389	−5.5218	0.0527
Speckled sanddab			
Citharichthys stigmaeus	[1]984.6	−5.4258	0.0527
California sheephead			
Pimelometopon pulchrum	[1]1,316	−5.4194	0.0527
Turbot			
Pleuronichthys decurrens	[1]1,065	−4.7059	0.0527
Pacific hake			
Merluccius productus	699.2	−4.1772	0.0527

[1] Time from stage III eggs.

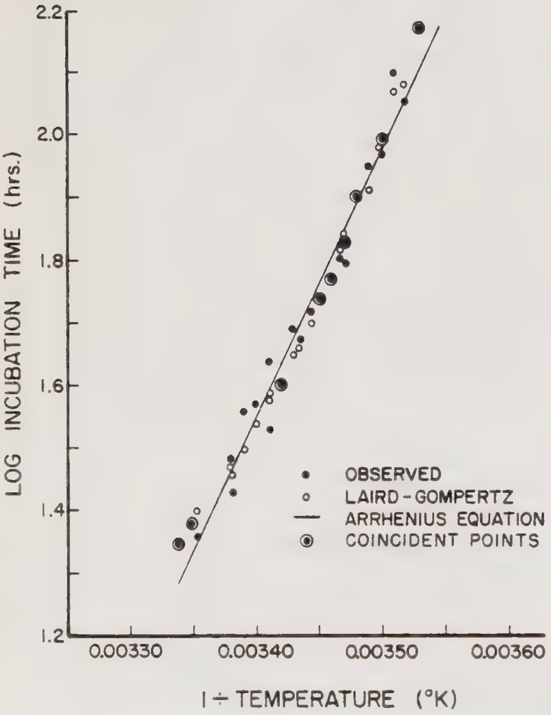

FIGURE 6.—A comparison of two methods of fitting the temperature-incubation time relationship in the northern anchovy.

larval anchovy, on the average, hatch at about 2.9 mm.

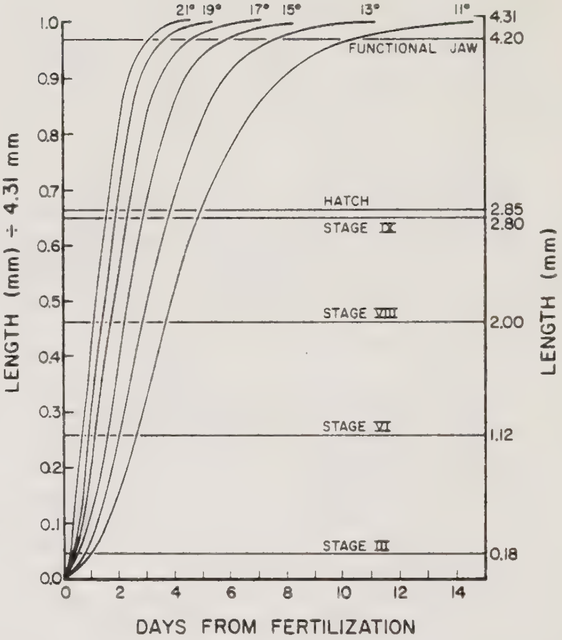

FIGURE 7.—Prehatch growth curves estimated from Equations (5) and (5a) for the northern anchovy.

Prehatch growth curves were obtained by fitting Equation (6) to hatch sizes of 2.85 at all observed temperatures as shown in Figure 7. Comparison with the sardine curves indicate that similar events (i.e., stages of development) occur relatively later for the anchovy. Observed and estimated event times are shown in Table 5.

Except for size at hatch, development data for the prehatch stage was not available for any other species. The curves may, if desired, be easily constructed from the parameters as shown in Table 6.

DISCUSSION

Nothing seems more true than the statement of Thompson (1942:158), "Every growth-problem becomes at last a specific one, running its own course for its own reasons. Our curves of growth are all alike—but no two are ever the same. Growth keeps calling our attention to its own complexity. . . . not least in those composite populations whose own parts aid or hamper one another, in any form or aspect of the struggle for existence."

The truth of this statement has been realized in the disappointing search for growth models derived from physiochemical processes. While it is true that the mathematical form of some equations arrived at from metabolic considerations are the same as those derived in other ways, more

TABLE 5.–Observed (Obs.) and estimated (Est.)[1] time in hours to developmental egg stages[2], hatch, and appearance of the functional jaw of the northern anchovy.

Kramer (unpubl. data)											Lasker (1964)		
Temp. (°C)	Stage III		Stage VI		Stage VIII		Stage XI		Incubation time		Temp. (°C)	Stage IV to hatch	
	Ops.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.	Obs.	Est.		Obs.	Est.
11.1	—	—	—	—	—	—	—	—	113	118.8	11	81	83
12.5	—	—	—	—	—	—	—	—	98	95.1	12	65	71
13.8	20	15.2	42	41.8	58	59.4	78	77.1	80	78.2	13	58	61
15.2	15	12.6	35	34.6	50	49.1	65	63.7	63	64.7	16.8	38	37
16.6	10	10.6	26	29.0	39	41.2	51	53.4	55	54.2	17.8	34	33
18.0	9	9.0	24	24.6	35	35.0	44	45.4	49	46.0	18.8	31	29
19.4	8	7.7	21	21.1	33	30.0	39	39.0	40	39.5	19.6	28	26
20.8	6	6.7	19	18.4	28	26.1	35	33.8	36	34.3	20.5	25	24

[1] Estimates obtained from Equation (7) with parameters as shown in Table 6.

[2] Egg stages are defined by Ahlstrom (1943).

TABLE 6.–Mathematical parameters for prehatch growth curves of six fishes. See text for notation.

Species	L_0	K	α_0	m	β	Average size at hatching
Trachurus symmetricus	0.0005	9.0986	0.0226	5.8338	0.0588	1.95
Sardinops sagax	0.0341	5.1918	0.0317	6.1876	0.0490	3.74
Engraulis mordax	0.0250	5.1493	0.0412	5.5338	0.0546	2.86
Citharichthys stigmaeus	0.1814	5.0600	0.0270	6.2898	0.0319	1.97
Oxyjulis californicus	0.0425	4.7164	0.0572	7.2126	0.0260	1.89
Pleuronichthys decurrens	0.1843	3.2915	0.0480	4.5184	0.0528	3.00

often than not no meaningful biological interpretation of the metabolic parameters can be made. The essence of the growth equation used here is genetically programmed processes of exponential growth and of exponential decay of the specific growth rate. The most probable source of exponential growth is, of course, self-multiplication of cells, the causes of decay are many but not well understood. Laird (1964, 1965a, b, 1966a, b, 1967) has shown that this kind of relationship offers a practical means of analyzing growth of all tumors, as well as embryonic and postnatal growth of a number of avian and mammalian species. We have shown that at least the early stages of the growth of fishes follows a similar pattern.

As with other organisms, several growth cycles exist in fishes. The number of such cycles which will be recognized is determined by the time scale of measurements. We have used three cycles: 1) from fertilization to hatching, 2) from hatch to onset of feeding, and 3) feeding larvae.

In addition, we have observed that the temperature specific growth follows a similar pattern, i.e., exponential increase with an exponential decay of the temperature specific growth rate. In some instances a temperature optimum exists beyond which the specific growth rate begins to decline, although this may be related to food requirements at onset of feeding. Further, we have observed that for the same spawn 1) the asymptotic limit of each growth cycle is independent of temperature and 2) the biological events such as developmental egg stages, hatching, functional jaw development, etc., occur at the same size at all temperatures.

Figure 8 shows posthatch growth curves of the sardine as 1) extrapolated from the prehatch curves and 2) obtained from posthatch data. Although the curves are quite similar at higher temperatures, differences in the lower temperature range are large. Nevertheless, the time to development of the functional jaw is much more accurately determined from the extrapolated curve, indicating an intrinsic process independent

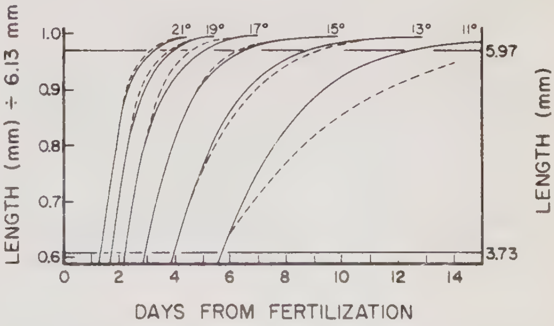

FIGURE 8.–Posthatch growth curves of the northern anchovy. Solid lines are extrapolated from prehatch curve. Broken lines are fitted to actual growth data.

of actual realized size. Comparison of the extrapolated curves for the sardine and anchovy, Figures 5 and 7, shows that for the same temperature and relative to the asymptotic size, hatching occurs later for the anchovy, but jaw development and first feeding occur at about the same time.

In summary, each growth cycle may be represented by an equation of the form

$$L = L_0 e^{K(1 - e^{-\alpha_T t})}$$

with

$$\alpha_T = \alpha_0 e^{\,m(1 - e^{-\beta T})}$$

or

$$\alpha_T = \alpha_{\text{opt}} e^{m_{\text{opt}}(1 - e^{-\beta \Delta})}$$

with

$$\Delta = |T - T_{\text{opt}}|$$

when a temperature optimum exists. The time required to attain a given size S is

$$t_S = \ln\left[\frac{K}{K - \ln(S/L_0)}\right] / \alpha_T$$

which has the same form as the original equation.

Most of the data available were from studies of two species, *Sardinops sagax* and *Engraulis mordax*, so that generalizations must be made with caution. Nevertheless, incubation times for several other species fit the model well.

Finally, it seems worthwhile to repeat that every growth problem becomes at last a specific one depending on many factors known or unknown, measureable or not. For example, time of fertilization will often not be known and age determinations will be inexact. Further, Hunter and Lenarz[7] have shown that egg size is a measurable and probably important factor in growth and survival of anchovy larvae. For feeding larvae, the quantity and quality of food is critical. Egg size appears to affect growth by a simple scale factor, all events being shifted up or down in proportion to the egg size. Variation in food may result in many "artificial" cycles when nutritional and caloric requirements are not met. Nevertheless, it seems clear that at least the early growth of many fishes may be described in terms of genetically determined but dynamically changing growth rates as defined by the Laird-Gompertz growth function.

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APPENDIX

The estimation procedure of Conway et al. (1970) is a least squares procedure which requires only the definition of the functional relationship and the first derivative with respect to each parameter. Although not stated explicitly, constant variance is assumed and, hence, the logarithmic form will be used throughout. For a single-cycle Laird-Gompertz curve the equations are as follows:

$$\ln F = \ln F_0 + A[1 - \mathrm{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{F_0} = 1/F_0$$

$$\frac{\partial \ln F}{A} = [1 - \mathrm{Exp}(-\alpha t)]/\alpha$$

$$\frac{\partial \ln F}{\alpha} = A[(\alpha t + 1)\,\mathrm{Exp}(-\alpha t) - 1]/\alpha^2$$

For a two-cycle curve with the second cycle beginning at $t = t^*$ the equations are:

$$\ln F = \ln F_0 + A[1 - \mathrm{Exp}(\alpha\Delta_1)]/\alpha + B[1 - \mathrm{Exp}(-\beta\Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial F_0} = 1/F_0$$

$$\frac{\partial \ln F}{\partial A_0} = [1 - \mathrm{Exp}(-\alpha\Delta_1)]/\alpha$$

$$\frac{\partial \ln F}{\partial \alpha} = A[(\alpha\Delta_1 + 1)\,\mathrm{Exp}(-\alpha\Delta_1) - 1]/\alpha^2$$

$$\frac{\partial \ln F}{\partial \beta} = [1 - \mathrm{Exp}(-\beta\Delta_2)]/\beta$$

$$\frac{\partial \ln F}{\partial \beta} = \beta[(\beta\Delta_2 + 1)\,\mathrm{Exp}(-\beta\Delta_2) - 1]/\beta^2$$

$$\frac{\partial \ln F}{\partial t^*} = [A\,\mathrm{Exp}(-\alpha\Delta_1) - B\,\mathrm{Exp}(-\beta\Delta_2)]$$

where $\Delta_1 = \mathrm{MIN}\,(t, t^*)$

$\Delta_2 = \mathrm{MAX}\,(t - t^*, 0)$.

FORTRAN programs are available for fitting single-cycle, temperature-dependent and multicycle, temperature-dependent curves at SWFC.

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